

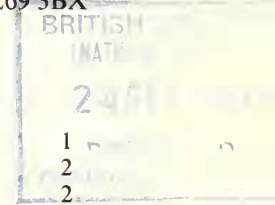
# *Puellina* (Bryozoa; Cheilostomata; Cribriliniidae) from British and adjacent waters

J. D. D. Bishop

Departments of Palaeontology and Zoology, British Museum (Natural History), Cromwell Road,  
London SW7 5BD

B. C. Househam

Department of Oceanography, University of Liverpool, Brownlow Hill, Liverpool L69 3BX



## Contents

Synopsis . . . . .	1
Introduction . . . . .	2
Material and methods . . . . .	2
Ovicell development . . . . .	4
Systematic account . . . . .	4
Generic and subgeneric definitions . . . . .	4
<i>P. gattyae</i> (Landsborough, 1852) . . . . .	7
<i>P. setosa</i> (Waters, 1899) . . . . .	11
<i>P. modica</i> n.sp. . . . .	16
<i>P. praecox</i> n.sp. . . . .	21
<i>P. directa</i> n.sp. . . . .	25
<i>P. venusta</i> Canu & Bassler, 1925 . . . . .	28
<i>P. innominata</i> (Couch, 1844). . . . .	33
<i>P. bifida</i> (d'Hondt, 1970) . . . . .	37
<i>P. arrecta</i> n.sp. . . . .	43
<i>P. flabellifera</i> (Kirkpatrick, 1888) . . . . .	48
<i>P. corbula</i> n.sp. . . . .	52
<i>P. pedunculata</i> Gautier, 1956 . . . . .	55
Discussion . . . . .	59
Acknowledgements . . . . .	61
References . . . . .	61

## Synopsis

*Cribrilaria* Canu & Bassler, 1929 is treated as a subgenus of *Puellina* Jullien, 1886, and *Glabrilaria* n.subgen. is established within *Puellina* to accommodate *P. pedunculata* Gautier, 1956 and related species. The following nine species of *Puellina* are recognised from British and adjacent waters: *P. arrecta* n.sp., *P. bifida* (d'Hondt, 1970), *P. corbula* n.sp., *P. directa* n.sp., *P. gattyae* (Landsborough, 1852), *P. innominata* (Couch, 1844), *P. modica* n.sp., *P. praecox* n.sp., and *P. venusta* Canu & Bassler, 1925. A table of key characters for the identification of these species is given. The distribution of *Puellina* around the British Isles shows a marked southerly and westerly bias. There seems to be no evidence for the occurrence of *P. setosa* (Waters, 1899) further north than the southern part of the Bay of Biscay.

A neotype is designated for *P. gattyae*. Lectotypes are selected for *Lepralia steindachneri* Heller, 1867 and *L. cribrata* Heller, 1867, both of which are junior synonyms of *P. gattyae*, and for *P. setosa*, *P. bifida*, *P. pedunculata* and *P. flabellifera* (Kirkpatrick, 1888).

*P. praecox* n.sp. also occurs in the Plio-Pleistocene Red Crag of eastern England. *P. venusta* is found as a fossil in the Badenian (Middle Miocene) of the Vienna Basin. *P. bifida* is extremely similar to *P. kollmanni* (David & Pouyet, 1974) from the Badenian of the Vienna Basin. *P. rarecostata* (Reuss, 1848) from the same rocks is intermediate in appearance between the two Recent species *P. setosa* and *P. modica*.

Three categories of ovicell development within the genus are noted, and their significance discussed.

## Introduction

Perhaps because of difficulties of observation caused by their small zooid size, there has been a tendency in the past to assign most Recent *Puellina* or *Cribrilaria* specimens to a limited number of nominal species within which extensive morphological variation has been accommodated. The wide limits of variation assigned to *Cribrilina radiata* by Hincks (1880) is a notable example of this approach. The subsequent task of refining species concepts within the group has been given impetus by the increased morphological detail available through the use of the Scanning Electron Microscope (SEM). This work was initiated by Harmelin (1970) in a revision of Mediterranean species and has been continued by the same author (1978; 1984) for NE. Atlantic and Mediterranean faunas.

The present paper is an account of Recent species from British and adjacent waters, in which mention is also made of relevant fossil material from the European Neogene. Following Gordon (1984), *Cribrilaria* is treated as a subgenus of *Puellina*. A new subgenus within *Puellina* is established for certain species formerly placed in *Cribrilaria*.

## Material and methods

Material studied during the present work is located in the following institutions:

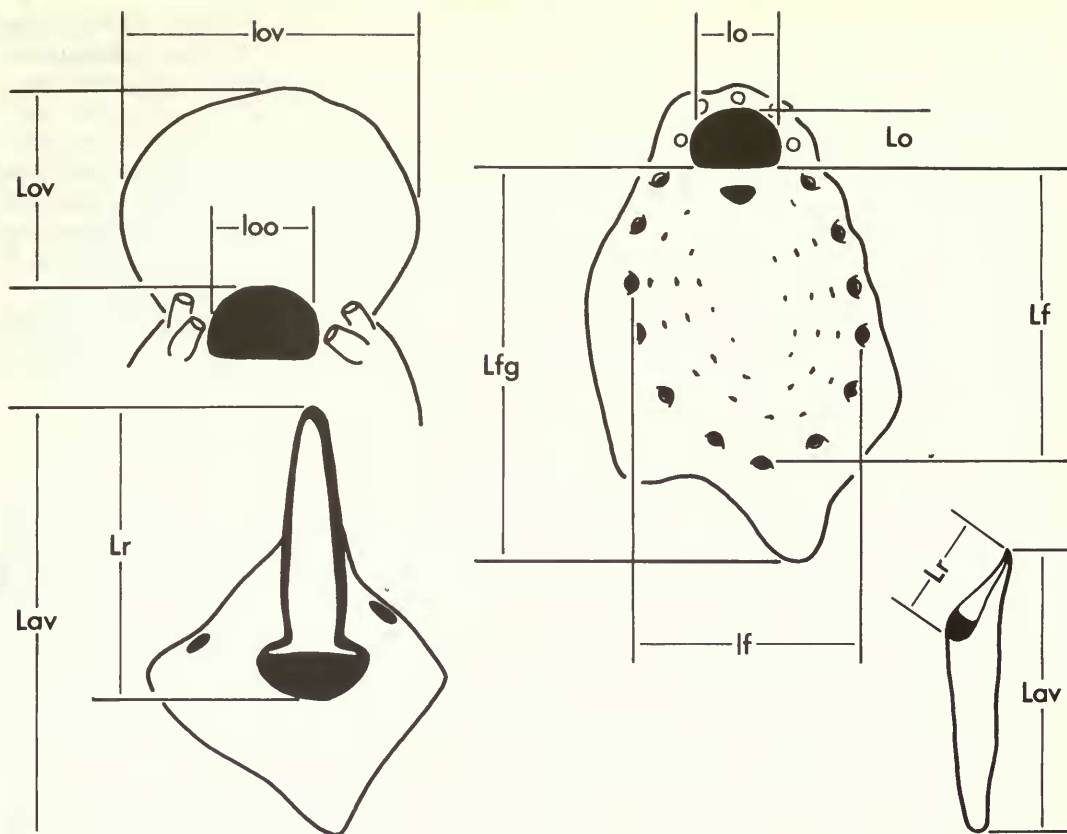
BMNH: British Museum (Natural History), London, U.K.; Recent specimens, Zoology Department; fossil specimens, Palaeontology Department.

IP: Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris, France; Canu Collection.

IZUI: Institut für Zoologie der Universität Innsbruck, Innsbruck, Austria; Heller Collection.

**Table 1** Details of Channel Stations

Station	Latitude	Longitude	Depth	Deposit
183	50°39.3'N	01°22.6'E	48 m	Clean coarse sand
230	49°36.3'N	03°26.7'W	75 m	Coarse shell sand
240	49°30.4'N	01°59.0'W	29 m	Coarse shell sand
247	49°10.8'N	02°52.1'W	64 m	Clean fine shell gravel, some stones
248	49°08.1'N	03°02.3'W	73 m	Clean fine shell gravel, some stones
249	49°05.1'N	03°13.5'W	77 m	Clean fine shell gravel, some stones
250	49°02.5'N	03°25.0'W	80 m	Stones, some clean fine shell gravel
251	49°00.0'N	03°36.5'W	77 m	Coarse shell sand, some stones
252	48°57.0'N	03°48.7'W	82 m	Clean shell gravel, some stones
253	48°52.2'N	03°54.0'W	79 m	Clean coarse sand, some gravel
256	48°50.7'N	04°13.1'W	91 m	Clean coarse shell sand, some stones
257	48°48.7'N	04°22.5'W	96 m	Clean coarse shell sand, some stones
258	48°46.2'N	04°30.7'W	99 m	Clean coarse shell sand, some stones
260	48°51.5'N	04°42.0'W	106 m	Coarse silty sand, some gravel and stones
261	49°00.0'N	04°44.5'W	101 m	Clean coarse shell sand, some gravel and stones
263	49°15.2'N	04°50.0'W	102 m	Coarse silty shell sand, some shells
275	49°38.2'N	01°00.0'W	38 m	Clean coarse sand, some gravel and stones
314	49°12.4'N	03°14.8'W	73 m	Clean shell gravel, some stones
315	48°57.5'N	04°00.7'W	88 m	Clean fine shell gravel, some stones
316	49°07.2'N	04°02.5'W	86 m	Stones, some clean fine shell gravel
317	49°18.0'N	04°04.2'W	86 m	Shell gravel, some stones
318	49°27.6'N	04°07.0'W	86 m	Clean coarse shell sand, some stones



**Fig. 1** Measurements on autozooids, interzooidal avicularia (bottom left) and erect avicularia (bottom right). Abbreviations: Lav = length of rostrum and frontal non-calcified area plus proximal gymnocyst of avicularium; Lf = length of frontal shield of autozooid; lf = width of frontal shield of autozooid; Lfg = length of frontal shield plus gymnocyst of autozooid; Lo = length of orifice of non-ovicellate autozooid; lo = width of orifice of non-ovicellate autozooid; loo = width of orifice of ovicellate autozooid; Lov = length of ovicell; lov = width of ovicell; Lr = length of rostrum plus frontal non-calcified area of avicularium.

LBIMM: Laboratoire de Biologie des Invertébrés Marins et de Malacologie, Muséum National d'Histoire Naturelle, Paris, France.

MM: Manchester Museum, Manchester, U.K.; microslide preparations from the Waters Collection.

NMV: Naturhistorisches Museum, Vienna, Austria.

Many of the records presented here are from encrusted shells collected during 1960 to 1962 for a study of the Recent benthos of the English Channel by Holme (1966), subsequently used for an account of bryozoan assemblages by Grant & Hayward (1986), and now deposited in the collections of the BMNH. Station details taken from Holme (1966) are given in Table 1. In the list of material examined for each species, these stations are referred to simply as 'Channel Stn . . .'; they are mostly on the French side of the Channel, with a few in mid-Channel. Locality details of other BMNH material are given as they appear on specimen labels or in the specimen catalogue; any additional information is given in square brackets.

SEM observations were made on uncoated material using an International Scientific Instruments model 60A with charge-free anticontamination system (CFAS). Images were generated at a

working voltage of 15 or 25 KV from back-scattered electrons using a Robinson detector. The magnifications of the resulting micrographs were calculated by light microscope calibration of each specimen, since the readings given by the SEM itself were inaccurate. Stereo pairs were taken at an angular separation of 10°.

Morphological measurements were taken from scanning electron micrographs. The measurements, and the abbreviations employed for them, are explained in Figure 1. Orifice width was measured to the proximo-lateral corners of the orifice. The papilla pores were taken to mark the edge of the frontal shield. Ovicell length was measured to the distal margin of the ovicell opening. The apertural bar was not included in counts of the number of costae. Values of the coefficient of variation (C.V.) were corrected as described by Simpson, Roe & Lewontin (1960:101, 102).

The term pluriserial is used in the descriptions below to indicate encrusting colonies forming lobes of fewer than about 10 autozooids abreast (Figs 29, 74). Multiserial colonies consist of broader lobes or extensive sheet-like growths.

### Ovicell development

In *Puellina*, and in many other cribrimorphs, the process of colony growth is apparently discontinuous, with pauses between the budding of successive zooid generations at the edge of the colony (Lidgard, 1985). Based on the timing of production of the ovicell in relation to the budding of the maternal autozooid and of the zooid distal to it, the following three categories of ovicell may be recognised in the species discussed here:

- A—The ovicell is produced during the budding of an autozooid distal to the maternal autozooid, and is a proximal component of the distal autozooid. Thus the completed ovicell never lies at the extreme edge of the colony. The frontal walls of the ovicell and of the distal autozooid are continuous. See Figures 40, 46, 50, 62 and 79.
- B—The ovicell is produced during the budding of a kenozooid (which has an area of costate frontal shield) distal to the maternal autozooid, and is a proximal component of the kenozooid. If the area of costate frontal shield is relatively small, the newly completed ovicell may lie very close to the extreme edge of the colony. The frontal walls of the ovicell and of the kenozooid are continuous. See Figures 70, 94, 95 and 96.
- C—The ovicell appears to be a distal component of the maternal autozooid, and is not associated with an area of kenozooidal costate frontal shield. Thus the newly completed ovicell lies at the extreme edge of the colony. Zooids distal to the maternal autozooid and ovicell are budded subsequently, and their frontal walls are separate from that of the ovicell. See Figures 2, 19, 23, 33 and 83.

Ovicells of category C of certain species have a number of uncalcified subcircular spots on the frontal surface (Figs 2, 12), similar in appearance when viewed by SEM to the pematidia of the costate frontal shield. These occur in a more or less regular arrangement, generally approximating to an outer ring of spots sometimes enclosing a number of others. This condition is referred to as punctate in the relevant descriptions below. In ovicells of category C of other species, and of categories A and B, small uncalcified patches sometimes occur on the frontal surface (Figs 50, 73), particularly on the crests of ridges and the tops of tubercles. However the size, shape and occurrence of these patches are inconstant and their spatial arrangement is relatively haphazard, and in such cases the ovicell is described below as non-punctate.

### Systematic account

#### Genus *PUELLINA* Jullien, 1886

Type species: *P. gattyae* (Landsborough, 1852), by original designation.

Jullien (1886), in addition to establishing *Puellina*, selected *Eschara radiata* Moll, 1803 as the type

species of *Cribrilina* Gray, 1848. Since *Lepralia punctata* Hassall, 1841 is the type species of *Cribrilina* by monotypy, Jullien's selection was invalid, but it did serve to indicate clearly that he excluded *E. radiata* from the genus *Puellina*. However, *E. radiata* is the type species of *Cribrilaria* Canu & Bassler, 1929, which is treated in the present paper as a subgenus of *Puellina*. The definition of the genus *Puellina* adopted here is therefore broader than Jullien's (1886), but coincides with that of Levinsen (1909), who referred *E. radiata* to the genus, and of Gordon (1984), who included *Cribrilaria* in *Puellina* as a subgenus. Jullien's original concept of the genus was in fact equivalent to that of the subgenus *Puellina* employed here.

REVISED DIAGNOSIS. Autozoid with pericystal frontal shield of fused but discernible spines (= costae) in more or less pinnate or radiating pattern; each costa generally with 1 or more small pematidia (= lumen pores); fusion of successive costae interrupted by 1 or more lacunae (= intercostal pores) which are short (i.e. do not take a slit-like form elongate parallel to the costae); non-calcified papilla (presumed to be evagination of frontal membrane) protruding from single papilla pore (bordered on one side by gymnocyst) between bases of successive costae around margin of frontal shield. Calcified (secondary) orifice D-shaped, with straight proximal edge, abutting similarly-shaped operculum around its entire margin; orifice without condyles, operculum hinged at extreme proximal edge. Apertural bar (presumed to be modified distalmost pair of costae) just proximal to orifice usually with 1 or more sub-oral (= sub-orificial) lacunae on midline between left and right components of bar. Oral (= orificial) spines erect, unfused, jointed at or near base, present around lateral and distal margins of orifice in non-ovicellate autozooids, restricted to lateral margins of orifice in ovicellate zooids. Autozooids with several pore chambers around distolateral and distal margins. Ovicell sub-globular, hyperstomial, cleithral. Avicularium (if present) with discrete gymnocystal cystid. Ancestrula tatiform, without pronounced cryptocyst, frequently regenerated as zoid with cribrimorph frontal shield.

The possession of non-calcified papillae protruding through papilla pores around the periphery of the frontal shield is regarded here as a synapomorphy of the genus *Puellina*.

### Subgenus *PUELLINA* Jullien, 1886

*Puellina* Jullien, 1886; 607.

*Puellina*: Prenant & Bobin, 1966; 597. Hayward & Ryland, 1979; 66. Harmelin, 1984; 81.

Type species: *P. gattyae* (Landsborough, 1852), by original designation. Other NE. Atlantic species included: *P. setosa* (Waters, 1899), *P. modica* n. sp.

Proximal gymnocyst of autozoid relatively broad; pericyst relatively small (approximately circular in outline). Oral spines without apophyses, each with brown chitinous articulation at base; 2 spines in ovicellate zooids (5 in non-ovicellate zooids). Setiform papillae from most distal pair of papilla pores. External uncalcified windows of pore chambers relatively small. Ovicell of category C (p. 4), punctate. No avicularia. Median proximal spine of ancestrula with simple (not bifid) tip; ancestrula regenerated as miniature autozoid (or kenozooid).

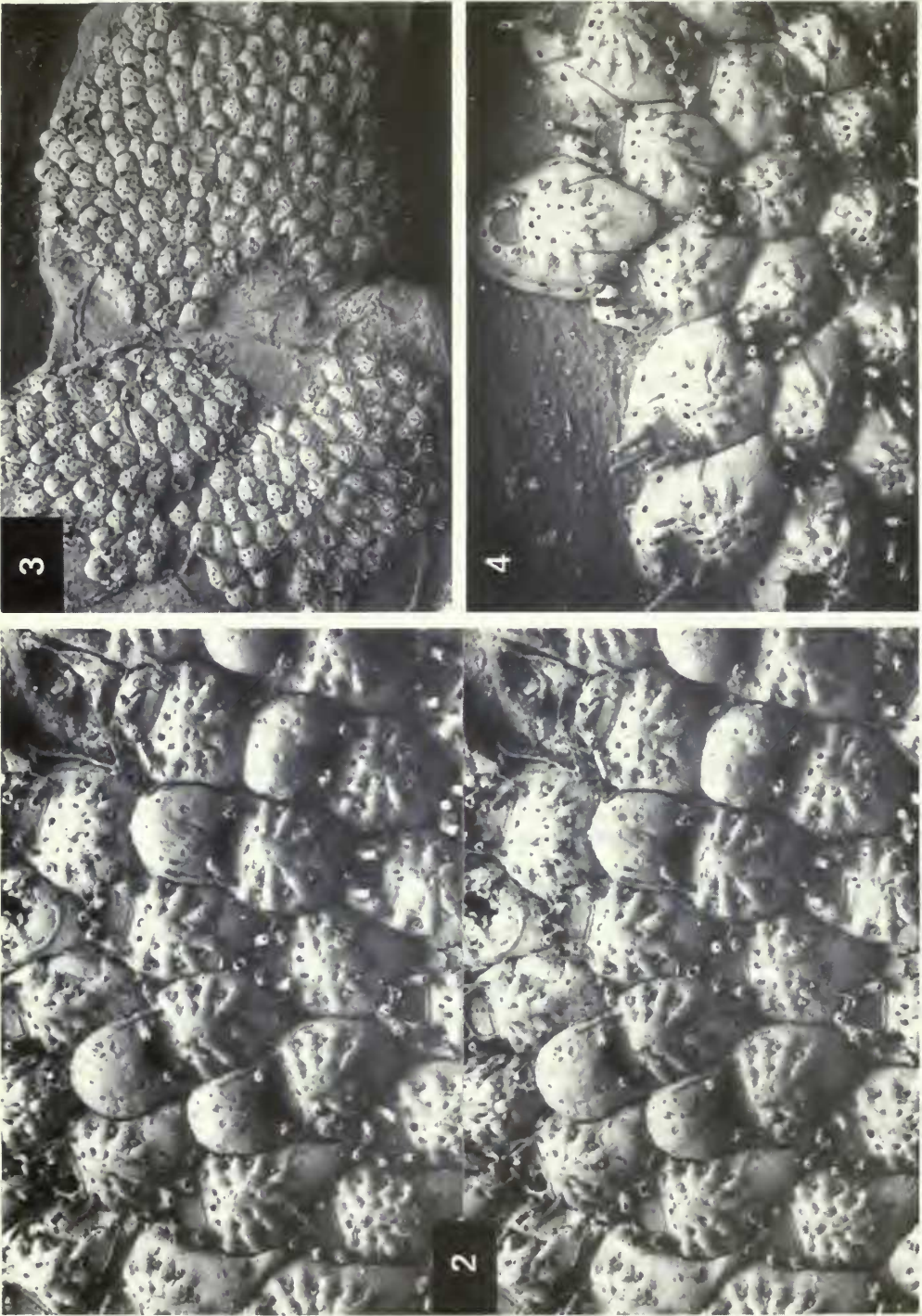
### Subgenus *CRIBRILARIA* Canu & Bassler, 1929

*Cribrilaria* Canu & Bassler, 1929; 33. (*Cribrilaria* Canu & Bassler, 1928; 27 is regarded as a *nomen nudum*.)

*Cribrilaria*: Hayward & Ryland, 1979; 62. Gordon, 1984; 63.

Type species: *P. radiata* (Moll, 1803), by original designation. NE. Atlantic species included: *P. venusta* Canu & Bassler, 1925, *P. innominata* (Couch, 1844), *P. bifida* (d'Hondt, 1970), *P. hexaspinosa* (Harmelin, 1978), *P. octospinosa* (Harmelin, 1978), *P. arrecta* n.sp.

Proximal gymnocyst of autozoid relatively narrow; pericyst relatively large. Oral spines with or without apophyses, bases not brown; 4 in ovicellate zooids. Setiform papillae from most distal pair of papilla pores. External uncalcified windows of pore chambers relatively large. Ovicell of category A (p. 4) (sometimes B in *P. bifida*), non-punctate. Avicularia interzooidal. Median proximal spine of ancestrula generally with bifid tip; ancestrula regenerated as kenozooid.



Figs 2-4 *Puellina gattiyae* (Landsborough): (2) stereo pair of neotype (BMNH 1854.11.15.125), Sidmouth,  $\times 81$ ; (3) whole colony, neotype,  $\times 19$ ; (4) edge of colony, BMNH 1897.5.1.623, South Devon,  $\times 80$ .

**Subgenus *GLABRILARIA* n.subgen.**

Type species: *P. pedunculata* Gautier, 1956. Other species included: *P. africana* (Hayward & Cook, 1983), *P. corbula* n.sp., *Cribrilaria pedunculata* in the sense of Harmelin (1968) (not Gautier, 1956), *P. cristata* (Harmelin, 1978).

Proximal gymnocyst of autozoid relatively narrow; pericyst relatively large. Oral spines without apophyses, bases not brown; 4 in ovicellate zooids. Ordinary (short) papillae from most distal pair of papilla pores. External uncalcified windows of pore chambers of moderate size. Ovicell of category B or C (p. 4), non-punctate. Avicularia small, erect or semi-erect, generally budded from single pore chamber. Median proximal spine of ancestrula with simple (not bifid) tip; ancestrula regenerated as kenozooid.

ETYMOLOGY. From a modification of *Cribrilaria*, from which the new subgenus is distinguished, combined with the Latin *glaber*, 'without hair' or 'smooth skinned', a reference to the absence of setiform papillae in this group.

***Puellina (Puellina) gattyae* (Landsborough, 1852)**

(Figs 2–10 and Table 2)

*Lepralia gattyae* Landsborough, 1852; 326, 327, pl. 18 fig. 71.

*Lepralia gattyae*: Busk, 1854; 73, 74, pl. 83 fig. 6.

*Lepralia steindachneri* Heller, 1867; 109, 110, pl. 2 fig. 5.

*Lepralia cribrosa* Heller, 1867; 109, pl. 2 fig. 6.

*Lepralia gattyae*: Waters, 1879; 36, pl. 9 fig. 6.

*Cribrilina gattyae*: Hincks, 1880; 198, 199, pl. 25 fig. 10.

not *Cribrilina gattyae*: Norman, 1903; 98 (as '*Gattyae*') 'form encrusting a shell', pl. 9 fig. 5.

not *Puellina gattyae* var. *balearica* Barroso, 1919; 340, 341, figs 1–5 (= *Collarina* sp.).

*Puellina gattyae*: Prenant & Bobin, 1966; 598–600, fig. 208I.

*Puellina gattyae*: Hayward & Ryland, 1979; 66, 67, fig. 18A–D.

*Puellina gattyae*: Harmelin, 1984; 81–82, 85–87, figs 2–4, 7.

**MATERIAL EXAMINED BY SEM.**

Neotype (designated here): BMNH 1854.11.15.125 (Sidmouth, [South] Devon).

BMNH: 1897.5.1.623 (South Devon, three colonies); 1899.7.1.1317A (Sidmouth); 1911.10.1.735A (Belfast, on shell).

IZUI: 135/9855 (Adriatic Sea, lectotype of *Lepralia steindachneri* Heller, 1867, selected here); 125/17021 (Adriatic Sea, lectotype of *Lepralia cribrosa* Heller, 1867, selected here).

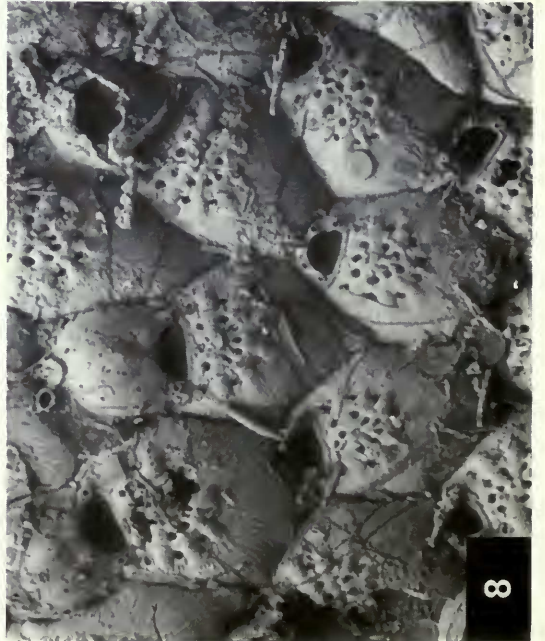
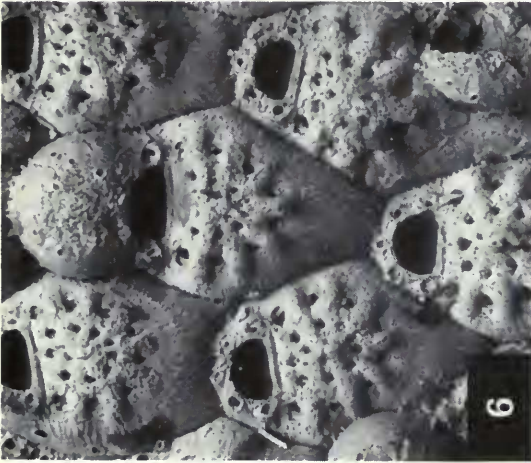
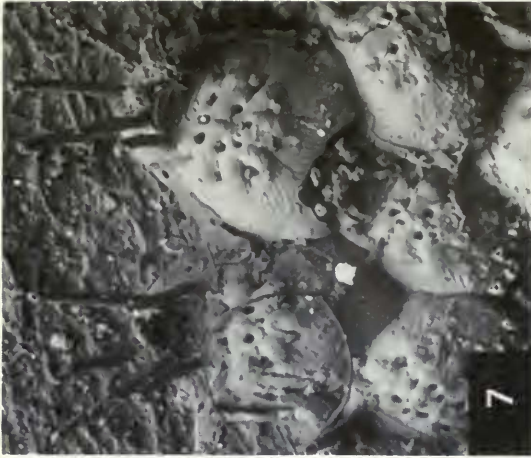
**OTHER MATERIAL.**

BMNH: 1879.4.25.17 (Naples); 1899.5.1.717 (Birterbuy [= Bertraghboy] Bay [Galway], labelled *Cribrilina punctata* var., colony on shell fragment 1); 1899.7.1.1317 and 1899.7.1.1318 (Sidmouth); 1899.7.1.1319 (Weymouth); 1911.10.1.734 (Naples); 1911.10.1.736 (British); 1975.1.12.444, 1975.1.12.518–522, 1975.7.1.5 and 1975.7.1.10 (Chios).

MM: 987 and 988 (Naples); 992 and 1171 (Menton).

**DESCRIPTION.** Colony encrusting, unilaminar, zooids distinct; largest colonies in available material multiserial, with a few hundred autozooids. Autozoid of variable shape in frontal view, generally sub-oval (longer than broad). Lateral gymnocyst of autozoid narrow or of moderate width; proximal gymnocyst broad, with proximal extension(s) between neighbouring zooids; gymnocyst with fine radiating striations.

Frontal shield (= pericyst) generally almost circular in outline, moderately to heavily calcified, slightly to strongly convex, with 5–9 costae (usually 7 or 8) fused extensively in centre of shield; central region of costal fusion may form blunt median umbo (frequently well developed in ovicellate zooids; Fig. 2). Each costa generally without clearly differentiated basal and subsequent portions, without distinct ornamentation; minute pelmatidium frequently seen near base, and larger pelmatidium occasionally near centre of shield. Intercoastal pores subcircular, of variable size, without denticles, usually only 1 pore between successive costae. Lipped papilla pore between bases of successive costae, larger than adjacent intercoastal pore.





Orifice of non-ovicellate autozoid D-shaped, clearly broader than long, proximal edge straight. Orifice of ovicellate zoid not appearing truncate in frontal view; width 1.1–1.2 times that of orifice of non-ovicellate zoid. Oral spines 5 in non-ovicellate zoid (6 in one disrupted autozoid of neotype), 2 in ovicellate zoid; with brown chitinous joint at base but without subsequent segmentation, without apophyses. Apertural bar sloping upwards to variable extent from proximal margin of orifice to first pair of costae; without tubercles; median suture and minute pelmatidium either side of midline occasionally discernible. Single median sub-oral lacuna, of variable shape and size although generally slightly larger than an intercostal pore, without denticles, flanked on either side by single intercostal pore (occasionally 2) slightly proximal to it.

Each autozoid with 6–8 distolateral pore chambers; uncalcified external windows of pore chambers (seen in zooids on edge of colony: Fig. 4) relatively small (about size of sub-oral lacuna).

Ovicell of category C (p. 4), length 1.0–1.2 times that of frontal shield of autozoid; frontal surface punctate, without ridges or discernible median suture.

Avicularium not present in available material.

Ancestrula (Fig. 9) tatiform, with median proximal spine overarching frontal surface plus 5 pairs of erect spines around edge of gymnocyst (i.e. total of 11 spines). Erect spines jointed at base; details of subsequent jointing (if any) not seen. Median proximal spine blunt-tipped and of relatively uniform thickness throughout length. Spines without inwardly directed (or other) apophyses. Ancestrula sometimes regenerated as small autozoid with 3 or 4 oral spines (Fig. 10).

**Table 2** *Puellina gattyae* (Landsborough): measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	47–51	48.7	3.17	9	Lf	99–150	130	8.87	24
b		45–53	48.1	6.32	8		124–155	140	10.0	10
c		42–49	45.5	12.3	2		88–97	94.0	5.99	3
d		43–47	44.4	4.43	7		100–148	124	11.5	15
a	lo	59–66	62.7	4.29	6	Lfg	193–301	235	13.2	24
b		65–70	67.6	3.55	8		237–390	279	19.3	10
c		56–60	58.0	5.49	2		193–222	211	8.18	3
d		57–75	64.4	15.8	5		218–346	273	14.9	14
a	loo	70–87	77.8	7.63	4	lf	115–169	140	10.5	24
b		85–88	86.5	2.76	2		108–147	132	8.80	10
c		—	—	—	0		84–111	94.3	16.8	3
d		72–87	80.3	7.21	7		93–157	125	18.3	15
a	Lov	123–155	138	8.14	10	lov	158–190	176	4.96	10
b		144–155	147	2.64	8		166–187	176	4.48	9
c		—	—	—	0		—	—	—	0
d		134–171	148	9.68	6		154–179	165	5.76	7

a = neotype (BMNH 1854.11.15.125); b = BMNH 1911.10.1.735A; c = IZUI 9855 (lectotype of *Lepralia steindachneri* Heller); d = IZUI 17021 (lectotype of *Lepralia cribrosa* Heller).

**Figs 5–10** *Puellina gattyae* (Landsborough): (5) non-ovicellate autozoid, BMNH 1897.5.1.623, South Devon,  $\times 163$ ; (6) ovicellate and non-ovicellate autozooids, BMNH 1911.10.1.735A, Belfast (on shell),  $\times 113$ ; (7) non-ovicellate autozooids, IZUI 135/9855, Adriatic (lectotype of *Lepralia steindachneri*),  $\times 123$ ; (8) ovicellate and non-ovicellate autozooids, IZUI 125/17021, Adriatic (lectotype of *Lepralia cribrosa*),  $\times 101$ ; (9) ancestrula, BMNH 1897.5.1.623, South Devon,  $\times 240$ ; (10) ancestrula regenerated as autozoid, BMNH 1899.7.1.1317A, Sidmouth,  $\times 290$ .

REMARKS. Type material of *Puellina gattyae* does not seem to have been formally recognised by previous authors. Despite this, there has apparently been little uncertainty concerning the identity of *P. gattyae* occurring on algae, although the synonyms *steindachneri* and *cribrosa* were created by Heller (1867), and Barroso (1919) erroneously assigned a new variety to the taxon. However there has been confusion, outlined below, regarding the occurrence of the species on hard substrata. *P. gattyae* also has at least two very close relatives, *P. setosa* (which has been the subject of considerable taxonomic uncertainty itself) and *P. modica* n.sp. Therefore an evaluation of possible type material is now considered worthwhile.

Landsborough (1852:326) introduced the name *Lepralia gattyae*, but attributed the name to Busk. Landsborough's description of the species was preceded by quotation marks and was stated (1852:326) to be 'from the pen of Mrs. Gatty', who, furthermore, was credited with the discovery of the species. It had been found (1852:327) on algae 'during two successive winters, at Sidmouth (1851 and 1852), and is to be met with also in Jersey'. Landsborough's figure (but not his text) was cited in Busk's (1854) account of *L. gattyae*; again the discovery of the species was credited to Mrs Gatty and material was reported from the same two localities, Sidmouth (Mrs Gatty) and Jersey (J. Alder).

Hence it would appear that the original concept of the species employed by both Landsborough and Busk was due to Mrs Gatty, and that the name *gattyae* was probably suggested to Landsborough by Busk. Despite the fact that Landsborough's use of the name appeared first, Busk has been cited, incorrectly, as the author of *Lepralia gattyae* by several subsequent workers, including Hincks (1880), Jullien (1886), Waters (1899), Levensen (1909), Barroso (1919) and Eggleston (1969). No collection of material associated with Landsborough's work is known. The Busk collection at the BMNH does not contain any material of the species from Jersey and only one microslide preparation, BMNH 1854.11.15.125, a single colony on alga from Sidmouth provided by Mrs Gatty, is undoubtedly contemporary with Busk's catalogue (1854). The label reads: 'Sidmouth G L. [~~coronata~~] Gattyae Pl. 83'. The letter 'G' on the label identifies Mrs Gatty as the source of the specimen, as may be confirmed by checking other microslides with this mark against the entries in Busk's catalogue; *Flustra coronata* Audouin had been likened by Busk (1854) to *L. gattyae*; plate 83 refers to the illustration of *L. gattyae* in Busk (1854). However, BMNH 1854.11.15.125 is not recognisable as the colony illustrated by either Landsborough or Busk. It is noted as 'type' in the MS species catalogue of the BMNH, but this supposed type status is presumed to stem from the specimen's connection with Busk's (1854) account rather than Landsborough's (1852). Although it is probable that this colony was part of the material on which Mrs Gatty based her description of the species published by Landsborough, it is not possible to prove this conclusively and it would not be valid to select it as lectotype. However, BMNH 1854.11.15.125 is clearly the best available indicator of the true nature of Landsborough's species, and in recognition of its significance it is selected here as neotype. The colony has lost much of its earlier growth, leaving two almost disjunct lobes totalling c. 200 autozooids.

Examination of IZUI specimen 135/9855 (Fig. 7) confirmed the conspecificity of *Lepralia steindachneri* Heller, 1867 and *P. gattyae*; this was first suggested by Waters (1879) and has been generally accepted by later authors. The arrangement of zooids in IZUI 135/9855 is reminiscent of Heller's plate 2 figure 5, but is not precisely the same; it is not known if this is the illustrated specimen. However, no other material attributable to Heller's account of this species is known (W. Schedl, Institut für Zoologie der Universität Innsbruck, pers. comm. to JDDB, 1986) and specimen 135/9855 is hereby selected as lectotype of *L. steindachneri*, confirming the established synonymy.

The identity of *L. cribrosa* Heller, 1867 has been uncertain in the past, but the name has been commonly cited as a junior synonym of *Collarina balzaci* (Audouin). However, Heller's figure (1867: pl. 2 fig. 6) shows setiform papillae, which are not present in *C. balzaci* auct. The type material received on loan (IZUI 125/17021; Fig. 8) is in fact referable to *P. gattyae*. Once again, it is not known if this is the specimen illustrated by Heller, but no other material referable to Heller's account is available (W. Schedl, Institut für Zoologie der Universität Innsbruck, pers. comm. to JDDB, 1986). IZUI 125/17021 is therefore selected as lectotype of *L. cribrosa*, the name of which passes into the synonymy of *P. gattyae*. Heller's Adriatic material (of both nominal species) and

the BMNH specimens from the Aegean (Chios) listed above have a relatively smaller, flatter, and more lightly calcified frontal shield than is generally seen in material from further west in the Mediterranean basin and from the NE. Atlantic. In the Chios specimens, the median umbo may be relatively narrow and pointed.

Whilst there has been little confusion concerning the identity of *P. gattyae* material growing on algae, the name has been applied to several taxa encrusting shells etc., apparently in the belief that the appearance of the species is transformed on hard substrata. In fact *P. gattyae* on shell (BMNH 1899.5.1.717 and 1911.10.1.735A: Fig. 6) looks much the same as on algae and has similar dimensions (Table 2). Norman (1903) contrasted a form he tentatively attributed to *P. gattyae* found on a shell from Guernsey with the form on algae. However, judging by the shape of the intercostal pores illustrated by Norman (1903: pl. 9 fig. 5), his shell form was certainly not *P. gattyae*. Grant & Hayward (1986) recorded *P. gattyae* on shells from the English Channel, but the species has not been found on re-examination of their material. It would appear that their records of *P. gattyae* refer largely to material of *P. modica* n.sp. Other material on shell substrates in the collections of the BMNH originally registered under the name *gattyae* has been incorrectly identified with one exception, 1911.10.1.735A; the remainder comprises *P. arrecta* n.sp., *P. bifida*, *P. corbula* n.sp. and, most commonly, *P. modica* n.sp.

*P. gattyae* has been widely reported in the Mediterranean, including the Adriatic and Aegean Seas. It is known from SW. England and the Channel Islands. The most northerly records that could be substantiated were both on shell, from Galway (BMNH 1899.5.1.717) and Belfast (BMNH 1911.10.1.735A).

### *Puellina (Puellina) setosa* (Waters, 1899)

(Figs 11–19 and Table 3)

not *Cribrilina radiata* var.  $\alpha$  Hincks, 1880; 186, 190 (= *Puellina modica* n.sp.).

not *Cribrilina radiata* 'with vibraculoid setae': Hincks, 1880; pl. 25 fig. 5 (= *Puellina innominata*).

*Cribrilina setosa* Waters, 1899; 8, 9.

not *Puellina setosa*: Osburn, 1950; 186, pl. 29 fig. 4.

*Puellina setosa*: Harmelin, 1968; 1196, 1198, fig. 3(3, 4).

not *Cribrilaria setosa*: Harmelin, 1970; part 88–91, fig. 1m, pl. 2 figs 4, 5 (= *C. cassidainsis* Harmelin, 1984).

not *Cribrilaria setosa*: Harmelin, 1978; 189 (= *C. cassidainsis* Harmelin, 1984).

*Puellina setosa*: Hayward & Ryland, 1979; 68, fig. 19A–D.

*Puellina setosa*: Harmelin, 1984; 81–82, 85–87, figs 1, 5, 6, 14.

#### MATERIAL EXAMINED BY SEM.

Lectotype (selected here): MM 1173 (Madeira, the colony occupying an extensive section of the upper margin of the shell fragment and touching a balanid barnacle near the right (narrower) end of the substrate, viewed with the microslide's labels the correct way up).

BMNH: 1911.10.1.727a–c (Fosse de Cap Breton, colonies on stone).

MM: 1173 (Madeira, two paralectotype colonies on same shell as lectotype); 1137 (Naples, three colonies on alga).

#### OTHER MATERIAL.

BMNH: 1911.10.1.727 (Fosse de Cap Breton, several colonies on stone).

MM: 1173 (Madeira, one paralectotype colony on same shell as lectotype); 989 and 1006 (Naples, both labelled *gattyae*).

**DESCRIPTION.** Colony encrusting, unilaminar, zooids distinct; largest colonies in available material multiseriate, with several hundred autozooids. Autozooid of variable shape in frontal view, generally sub-oval (longer than broad), occasionally proximally bifid. Gymnocyst of autozooid narrow distolaterally, of moderate width proximolaterally, and broad proximally, with proximal extension(s) between neighbouring zooids; gymnocyst often with fine radial striations.

Frontal shield (= pericyst) generally almost circular in outline, moderately calcified, with little or no differential median thickening, with 7–12 costae (usually 9 or 10). Each costa with broad, very short, moderately ascending basal portion at periphery of frontal shield leading to tapering, nearly horizontal subsequent portion contributing to slightly convex central region of shield.

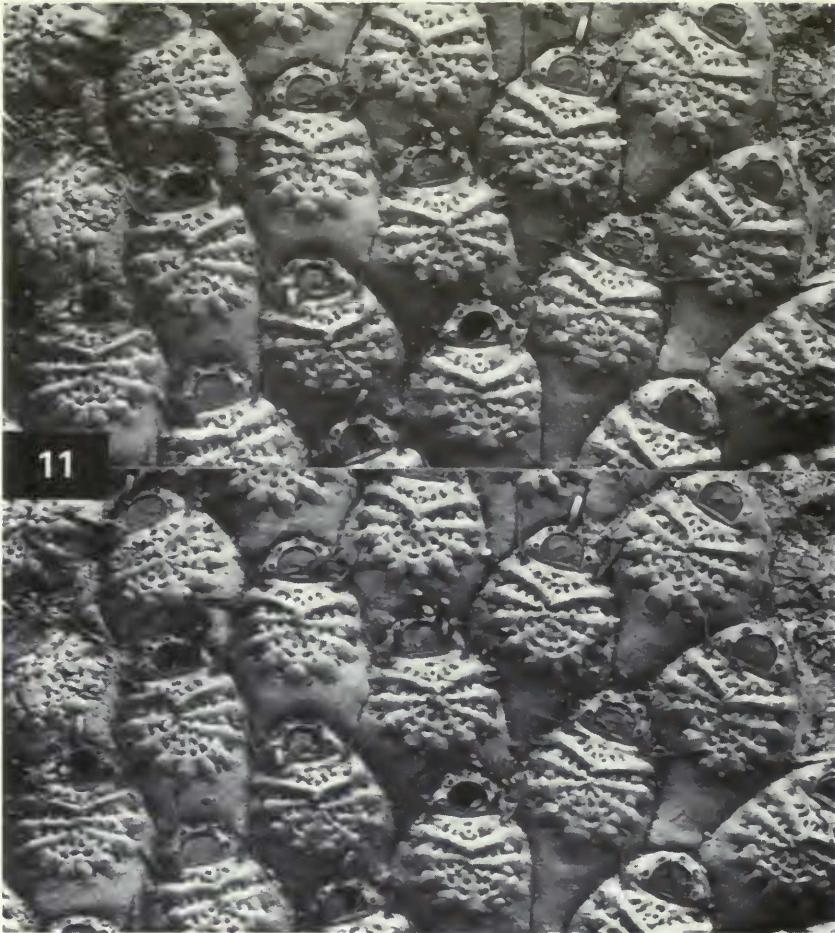
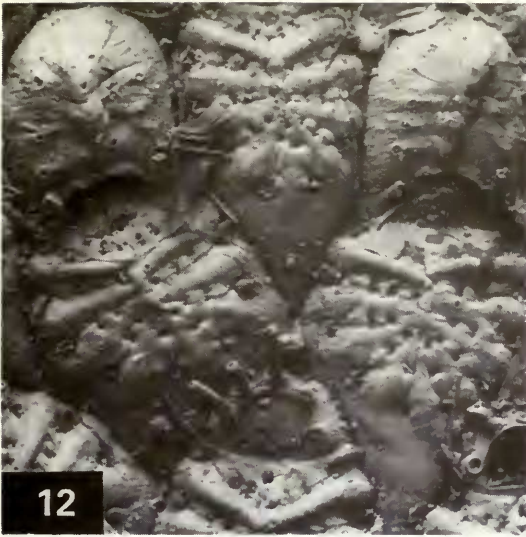


Fig. 11 *Puellina setosa* (Waters): stereo pair of BMNH 1911.10.1.727c, Fosse de Cap Breton,  $\times 73$ .

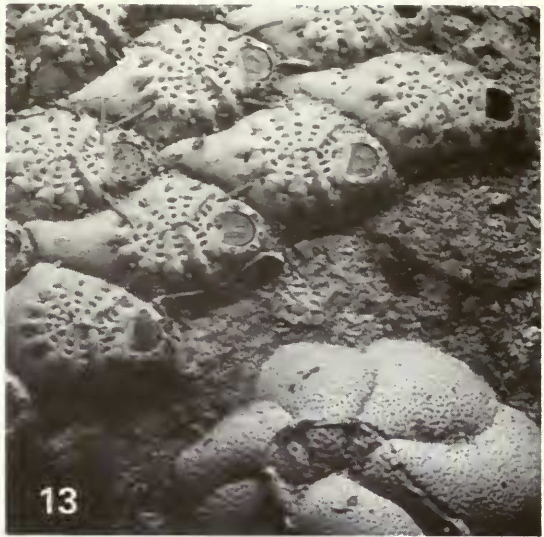
Costae without distinct ornamentation; first pair slightly prominent (sometimes forming very small median umbo), remainder low. Each costa frequently with pelmatidium near centre of shield and smaller pelmatidium near base. Intercostal pores sub-rectangular or reniform, relatively uniform in size throughout shield, often with denticle (sometimes 2) adjacent to intercostal suture; usually 2 or 3, occasionally 4, pores between successive costae. Lipped papilla pore between successive costae, about same size as adjacent intercostal pore.

Orifice of non-ovicellate autozooid D-shaped, slightly broader than long, proximal edge straight. Orifice of ovicellate zooid not appearing truncate in frontal view; width 1.2–1.3 times that of orifice of non-ovicellate zooid. Oral spines 5 in non-ovicellate zooid, 2 in ovicellate zooid; with brown chitinous joint at base but without subsequent segmentation, without apophyses. Apertural bar sloping slightly upwards from proximal margin of orifice to first row of intercostal pores, with pelmatidium on either side of median suture; without tubercles. Median sub-oral lacuna, about same size as an intercostal pore, frequently with denticle (occasionally 2) on proximal margin; one colony, BMNH 1911.10.1.727c, frequently with second, smaller median lacuna proximal to first lacuna and immediately distal to first row of intercostal pores.

Each autozooid with *c.* 8 distolateral pore chambers; uncalcified external windows of pore



12



13

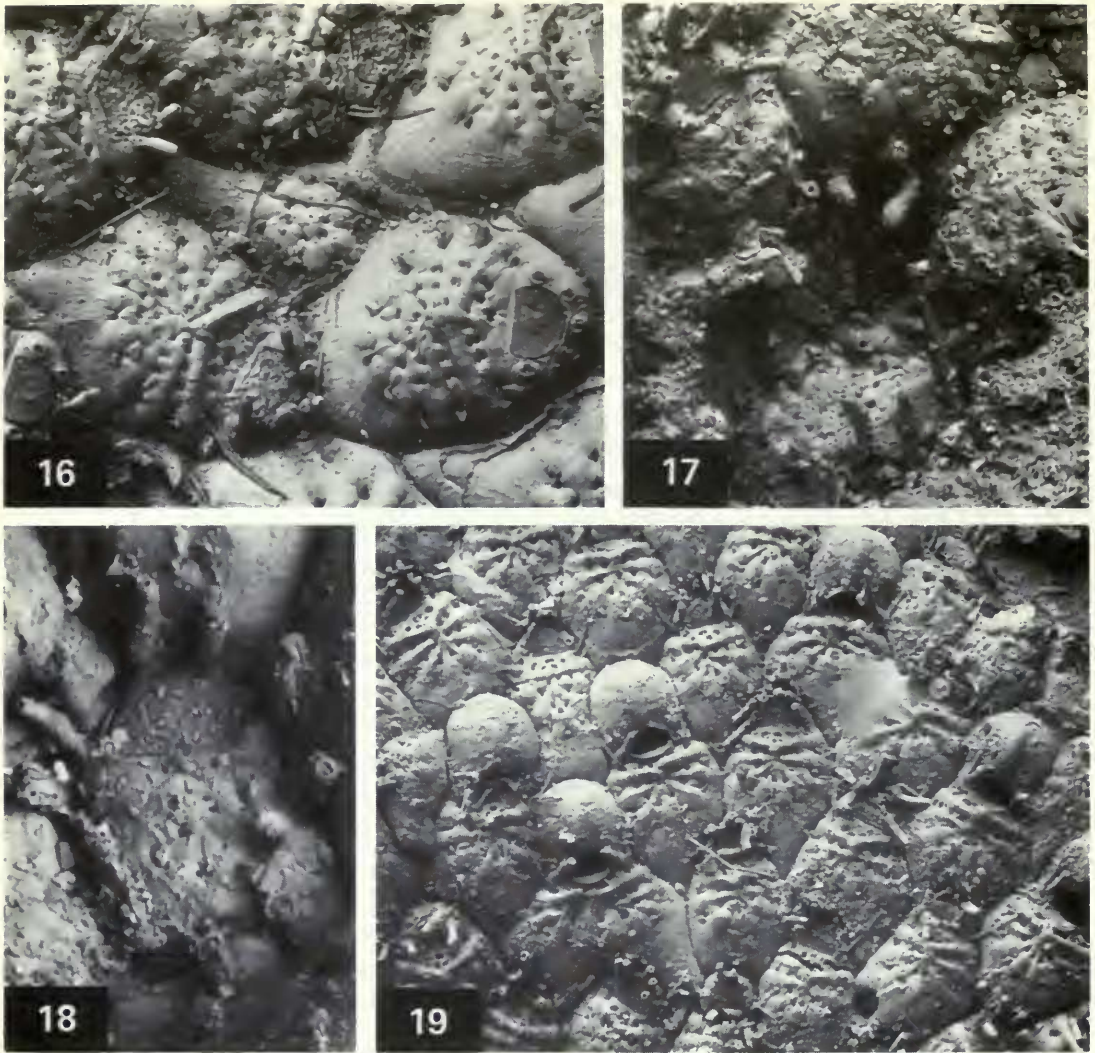


14



15

**Figs 12–15** *Puellina setosa* (Waters): (12) ovicellate autozooids, BMNH 1911.10.1.727b, Fosse de Cap Breton,  $\times 127$ ; (13) edge of colony viewed at angle, BMNH 1911.10.1.727c, Fosse de Cap Breton  $\times 70$ ; (14) non-ovicellate autozoid, same colony,  $\times 144$ ; (15) ovicellate and non-ovicellate autozooids, lectotype (MM 1173), Madeira,  $\times 101$ .



**Figs 16–19** *Puellina setosa* (Waters): (16) kenozooid and non-ovicellate autozooids, BMNH 1911.10.1.727b, Fosse de Cap Breton,  $\times 125$ ; (17) ancestrula (distal end faces bottom left), paralectotype (MM 1173), Madeira,  $\times 190$ ; (18) ancestrula regenerated as autozooid, lectotype (MM 1173), Madeira,  $\times 290$ ; (19) ovicellate and non-ovicellate autozooids, MM 1137, Naples,  $\times 60$ .

chambers (seen in zooids on edge of colony: Fig. 13) relatively small (only slightly larger than an intercostal pore).

Ovicell of category C (p. 4), length 0.8–1.0 times that of frontal shield of autozooid (sometimes 1.1 times in MM 1137, Naples); frontal surface punctate, frequently with very low median ridge, without discernible median suture.

Avicularium not present in available material.

Kenozooid (Fig. 16) infrequent, of variable size and shape, with cribrimorph frontal shield of costae in radiating pattern.

Ancestrula (Fig. 17) tatiform, with median proximal spine overarchng frontal surface plus 5 pairs of erect spines around edge of gymnocyst (i.e. total of 11 spines). Details of jointing (if any) of

spines not seen. Median proximal spine broad near tip. Spines without inwardly directed (or other) apophyses. Ancestrula sometimes regenerated as small autozooid (BMNH 1911.10.1.727a and lectotype: Fig. 18) which may lack oral spines, or sometimes as kenozooid (MM 1137, largest colony).

REMARKS. When Waters (1899) introduced the name *Cribrilina setosa*, he included only *Cribrilina radiata* var.  $\alpha$  Hincks (1880) in the synonymy of the new species. It is therefore apparent that the specific name *setosa* was intended to replace Hincks' appellation var.  $\alpha$ . However, there is no suggestion in Waters' unillustrated account that he actually examined material considered by Hincks to belong to var.  $\alpha$ , and no specimen labelled *C. radiata* var.  $\alpha$  is to be found amongst Hincks' material in the BMNH. The only indication concerning material available to Waters is as follows (1899:8): 'From an examination of specimens from Madeira and Naples, I cannot agree in calling this form with vibraculæ a variety of *radiata*.' No type material of *Cribrilina setosa* seems to have been formally recognised by later authors. The Madeiran collection which formed the main subject matter for Waters' paper was stated (1899:7) to have been sent by J. Y. Johnson. Microslide MM 1173 is labelled in Waters' hand as follows: 'Cribrilina setosa. Waters. Madeira. J.Y.J.'s coll. ovicell 0.24 & Crib. Balzaci no suboral pore'. There is thus little doubt that this was part of the material described by Waters, even though there is no reference to the publication and no designation as type material on the labels. (A section on *Cribrilina balzaci* followed that on *C. setosa* in

Table 3 *Puellina setosa* (Waters): measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	48-58	53.3	6.28	10	Lf	150-237	196	11.1	21
b		52-58	56.3	4.17	6		160-235	197	11.9	14
c		56-58	56.6	1.66	5		157-173	167	4.01	6
d		54-59	56.6	3.48	7		143-191	170	7.71	19
e		58-64	61.1	4.31	7		180-238	202	9.30	10
f		54-60	57.4	3.78	10		177-206	191	4.54	16
a	lo	56-70	62.5	5.67	13	Lfg	201-367	280	15.4	21
b		58-66	63.3	5.83	8		242-397	301	14.2	12
c		62-73	67.4	6.67	5		294-324	308	4.65	5
d		71-78	74.6	4.63	5		266-347	305	7.66	18
e		62-78	71.6	7.34	8		242-374	318	14.8	8
f		69-75	71.8	3.61	10		272-418	328	11.3	16
a	loo	—	—	—	0	lf	140-207	181	11.3	21
b		77	—	—	1		170-216	192	9.36	8
c		—	—	—	0		146-167	154	4.71	8
d		93-99	97.0	3.10	4		154-269	190	15.3	18
e		94-96	95.0	1.68	2		162-220	188	9.12	10
f		—	—	—	0		177-199	190	3.29	17
a	Lov	—	—	—	0	lov	—	—	—	0
b		125-158	150	9.93	5		177	—	—	1
c		—	—	—	0		—	—	—	0
d		157-183	171	5.57	7		190-200	196	2.46	7
e		174-181	178	3.14	2		172-176	174	1.83	2
f		—	—	—	0		—	—	—	0

a = lectotype (MM 1173); b = paralectotype (MM 1173); c and d = MM 1137 (2 colonies); e = BMNH 1911.10.1.727b; f = BMNH 1911.10.1.727c.

Waters' paper.) Microslide MM 1137 is labelled in Waters' hand: 'Cribrilina [*setosa* Wat. crossed out] [*Gattyae* crossed out] Off Nisida Naples. 30 metres 30/10/[*'87* crossed out] 79 5 spines without lateral avicularia or vibracula *radiata*'. There is therefore less evidence to connect this microslide directly with Waters' account, and Waters was apparently unsure of the identity of his Mediterranean material (which is nevertheless considered here to be conspecific with MM 1173 from Madeira). No other material labelled *setosa* has been located in the Waters Collection. Accordingly, the lectotype (Figs 15, 18) has been selected from the colonies on MM 1173.

Waters' material (MM 1173 and 1137, including the lectotype) is not in fact considered to be the species named *Cribrilina radiata* var. *a* by Hincks (1880:186). The number of costae on the frontal shield of the material from Madeira and Naples clearly exceeds that specified in Hincks' account, the arrangement of costae does not recall that described by the earlier author, and the ovicell of *Puellina setosa* does not bear nodular projections. Hincks' variety is considered to be the form named *Puellina modica* n.sp. below (see the Remarks on that species).

Osburn (1950) referred *Cribrilina setosa* to *Puellina*. Soule (1959) noted that at least part of Osburn's material had vicarious avicularia. The identity of the Pacific form with the specimens described by Waters is at best extremely doubtful, but Osburn's generic assignment is nevertheless correct with respect to Waters' material.

The illustrations of *P. setosa* by Hayward & Ryland (1979: fig. 19) are of BMNH 1911.10.1.727. The ancestrula they figured (1979: fig. 19D) has in fact regenerated as an autozoid, as suggested by Harmelin (1984) and Aristegui (1984). A similar regeneration in the lectotype is illustrated in the present paper (Fig. 18).

As noted by Waters (1899), *P. setosa* is very similar to *P. gattyae*. *P. setosa* may be distinguished from *P. gattyae* by the presence of more than 1 intercostal pore between successive costae; by the sub-rectangular or reniform shape of the intercostal pores, which have denticles (cf. rounded, without denticles); by the absence in all zooids of a well developed median umbo; and by the relatively less extensive proximal gymnocyst. Furthermore, the most distal pair of costae are slightly more prominent than the rest in *P. setosa*, a pattern not seen in *P. gattyae*.

In the Mediterranean, well documented records of *P. setosa* exist from the French coast, Naples, the Sicilian Channel and Greece (Waters, 1899; Harmelin, 1968; 1984). The species was recorded from Madeira by Waters (1899) and from the Canaries by Aristegui (1984). Having discounted *Cribrilina radiata* var. *a* Hincks, 1880 (see above), the most northerly Atlantic record for *P. setosa* that could be substantiated was from Fosse (= Gouf) de Cap Breton in the southern part of the Bay of Biscay (BMNH 1911.10.1.727). In view of the uncertainty that has surrounded the identity of the species, the record from the Irish Sea near the Isle of Man by Eggleston (1969) must be regarded as extremely doubtful. There seems to be no real evidence that the species occurs in British or adjacent waters.

### *Puellina (Puellina) modica* n.sp.

(Figs 20–28 and Table 4)

*Lepralia innominata*: Busk, 1854; pl. 86 fig. 3 (= BMNH 1847.9.16.79).

*Cribrilina radiata* var. *a* Hincks, 1880; 186, 190.

not *Cribrilina radiata* 'with vibraculoid setae': Hincks, 1880; pl. 25 fig. 5 (= *P. innominata*).

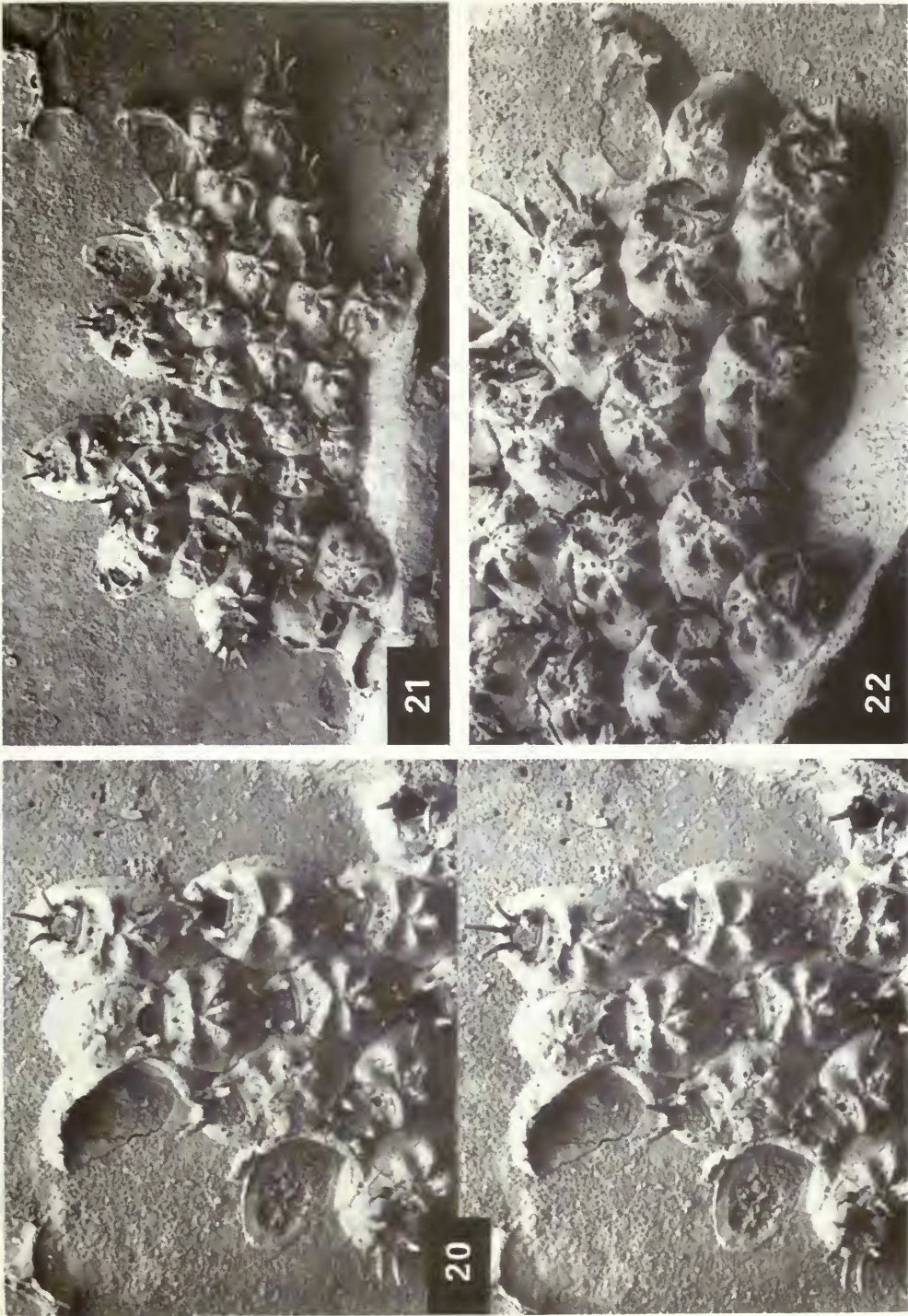
Holotype: BMNH 1985.11.20.58 (Channel Stn 249, 49°05'1"N 03°13'5"W, 77 m).

Paratypes (examined by SEM): BMNH: 1847.9.16.79 (British); 1936.12.30.331C (no locality [probably Liverpool Bay]); 1936.12.30.335A–C (Liverpool Bay); 1985.11.20.46 (Channel Stn 230); 1985.11.20.69i and 1985.11.20.71b,c (Channel Stn 252); 1985.11.20.106a,b (Channel Stn 275); 1985.11.20.112b (Channel Stn 315).

#### OTHER MATERIAL.

BMNH: 1847.9.16.139 and 1847.9.18.66 (British); 1899.5.1.1028 (Antrim, colony on shell A); 1899.5.1.1089 (Antrim, colony on shell A); 1899.5.1.1387 (Antrim, deep water); 1911.10.1.737C,D (Guernsey); 1936.12.30.329A–C (Isle of Man); 1963.2.12.349 (Hastings); 1985.11.20.50b,c and 1985.11.20.51 (Channel Stn 247); 1985.11.20.52f and 1985.11.20.54h (Channel Stn 248); 1985.11.20.55 and 1985.11.20.57c (Channel Stn 249); 1985.11.20.60b, 1985.11.20.61b, 1985.11.20.63c and 1985.11.20.64i–m (Channel Stn 250);





Figs 20–22 *Puellina modica* n. sp., holotype (BMNH 1985.11.20.58), Channel Stn 249: (20) stereo pair,  $\times 75$ ; (21) whole colony,  $\times 51$ ; (22) edge of colony viewed at angle,  $\times 100$ .

1985.11.20.65b, 1985.11.20.66 and 1985.11.20.67c (Channel Stn 251); 1985.11.20.69j-m, 1985.11.20.70b-d, 1985.11.20.71d and 1985.11.20.72l (Channel Stn 252); 1985.11.20.85b, 1985.11.20.87c,d and 1985.11.20.88c-h (Channel Stn 257); 1985.11.20.91c-h, 1985.11.20.92b, 1985.11.20.93b, 1985.11.20.94e, 1985.11.20.95a-e, 1985.11.20.96b,c and 1985.11.20.98c (Channel Stn 258); 1985.11.20.100d (Channel Stn 260); 1985.11.20.104i (Channel Stn 263); 1985.11.20.105h,i and 1985.11.20.106c,d (Channel Stn 275); 1985.11.20.108e,f (Channel Stn 314); 1985.11.20.115 (Channel Stn 317); 1985.11.20.116l (Channel Stn 318).

**DESCRIPTION.** Colony encrusting, unilaminar, zooids distinct; largest colonies in available material pluriserial to multiserial, with over 100 autozooids. Autozoid of variable shape in frontal view, generally round or sub-oval (longer than broad). Lateral gymnocyst of autozoid of moderate width or broad; proximal gymnocyst broad, frequently with short proximal extension(s) between neighbouring zooids; gymnocyst often with fine radial striations.

Frontal shield (= pericyst) generally almost circular in outline, moderately to heavily calcified, with little or no differential median thickening and no umbo, slightly convex, with 4-6 (most commonly 5) short tapering costae converging towards single point on midline. Each costa without clearly differentiated basal and subsequent portions; costal ridge, with longitudinal crest, occupying almost entire length of costa and generally decreasing gradually in height from periphery to centre of shield; without tubercles. Most distal pair of costae forming very shallow V in frontal view, with their costal ridges sometimes continuous from side to side. Intercostal pores sub-rectangular or reniform, small, relatively uniform in size throughout shield, often with denticles adjacent to intercostal suture; 1 or 2 pores between successive costae. Lipped papilla pore between bases of successive costae, larger than adjacent intercostal pore.

Orifice of non-ovicellate autozoid D-shaped, slightly broader than long, proximal edge straight. Orifice of ovicellate zooid not appearing truncate in frontal view; width 1.1-1.2 times that of orifice of non-ovicellate zooid. Oral spines 5 in non-ovicellate zooid, 2 in ovicellate zooid; with brown chitinous joint at base but without subsequent segmentation, slightly curved or straight, without apophyses. Apertural bar without marked proximal-distal slope; frequently with minute pelmatidium on each side of median suture; without tubercles. (Pelmatidia not observed elsewhere on shield.) Single, large, median sub-oral lacuna (Fig. 24), considerably larger than an intercostal pore, frequently with pair of denticles on proximal margin.

Each autozoid with 5-8 lateral and distolateral pore chambers; uncalcified external windows of pore chambers, seen in zooids on edge of colony, relatively small (slightly smaller than sub-oral lacuna).

Ovicell of category C (p. 4), length 1.2-1.5 times that of frontal shield of autozoid; frontal surface punctate, uncalcified spots being borne on *c.* 5 indistinct ridges in more or less radiating pattern or on tubercles; median suture occasionally discernible.

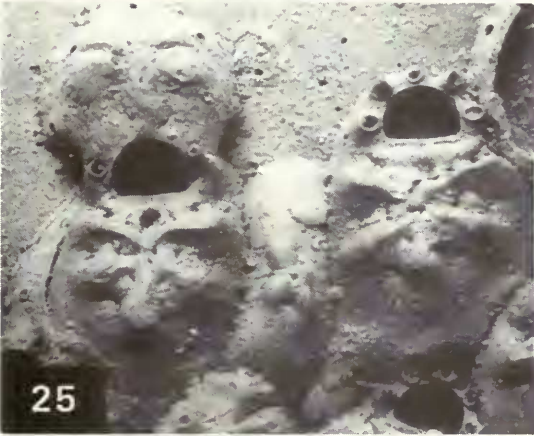
Avicularium not present in available material.

Kenozooid (Fig. 25) infrequent; single example seen, smaller than an autozoid, with rudimentary cribrimorph frontal shield of costae in more or less radiating pattern.

Ancestrula (Figs 26, 28) tatiform, with median proximal spine overarching frontal surface plus 5 pairs of erect spines around edge of gymnocyst (i.e. total of 11 spines). Erect spines jointed at base; subsequent segmentation not observed. Median proximal spine tapering towards tip (not bifid). Spines without apophyses. Ancestrula sometimes regenerated as autozoid (Fig. 27) or kenozooid.

**ETYMOLOGY.** *L. modicus*—not very large, humble; referring to the modest size of both zooids and colonies of this species.

**REMARKS.** In addition to the *radiata* and *innominata* forms, Hincks (1880) included three varieties,  $\alpha$ ,  $\beta$  and  $\gamma$ , in his concept of *Cribrilina radiata*. *Cribrilina radiata* var.  $\alpha$  was originally characterised (Hincks, 1880: 186) by its very small zooids, each with 5 very prominent costae on the frontal shield; the distal pair of costae formed a 'wall' proximal to the orifice; the ovicell bore nodular projections. Hincks also mentioned the presence of two slender vibraculoid setae (i.e. setiform papillae) in var.  $\alpha$ , and this observation alone was taken to characterise the taxon by subsequent workers. Hincks made no reference to any particular figure in his account. Nevertheless a number of later authors seem to have taken Hincks' plate 25 figure 5 to depict var.  $\alpha$ , although only



**Figs 23–28** *Puellina modica* n.sp.: (23) ovicellate and non-ovicellate autozooids at edge of colony, BMNH 1985.11.20.71c, Channel Stn 252,  $\times 97$ ; (24) distal part of non-ovicellate autozoid, same specimen,  $\times 310$ ; (25) kenzoozoid, ovicellate and non-ovicellate autozooids, BMNH 1985.11.20.106a, Channel Stn 275,  $\times 148$ ; (26) ancestrula, holotype (BMNH 1985.11.20.58), Channel Stn 249,  $\times 250$ ; (27) ancestrula regenerated as autozoid, BMNH 1985.11.20.46, Channel Stn 230,  $\times 250$ ; (28) ancestrula, BMNH 1985.11.20.69i, Channel Stn 252,  $\times 181$ .

**Table 4** *Puellina modica* n.sp.: measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	42-55	47.6	8.17	9	Lf	111-148	125	9.70	12
b		48-57	52.9	5.41	15		108-149	127	8.92	21
c		46-52	48.0	6.19	5		111-136	124	8.76	5
d		47-49	48.0	1.54	5		104-137	120	6.93	16
a	lo	53-60	56.3	4.13	8	Lfg	178-272	229	13.6	12
b		56-65	59.9	4.92	17		192-319	234	12.7	20
c		57-64	60.6	4.68	5		171-226	202	12.5	5
d		59-64	61.7	4.42	3		177-247	203	9.82	16
a	loo	61-69	65.0	9.79	2	lf	89-118	105	8.44	12
b		69-72	69.6	2.03	5		93-124	105	8.17	20
c		—	—	—	0		89-106	100	7.23	5
d		70	70.0	0.00	2		84-113	101	8.82	13
a	Lov	137-141	139	2.30	2	lov	141-151	146	5.45	2
b		140-158	147	5.57	4		173-200	183	6.73	5
c		—	—	—	0		—	—	—	0
d		137-151	143	4.81	4		135-167	153	8.66	5

a = holotype (BMNH 1985.11.20.58); b = BMNH 1847.9.16.79; c = 1936.12.30.335B; d = BMNH 1985.11.20.71c.

Hayward & Ryland (1979) categorically stated this interpretation of the figure, while Prenant & Bobin (1966) seemed to attribute a similar opinion to Osburn (1950). The figure was apparently assumed to portray var. *α* because the legend stated [*Cribrilina radiata*] 'with vibraculoid setae'. Waters (1899) introduced the name *Cribrilina setosa* with the apparent intention of elevating *Cribrilina radiata* var. *α* Hincks, 1880 to specific rank. The name *setosa* has accordingly been used subsequent to its introduction for material considered to resemble Hincks' plate 25 figure 5 and with conspicuous setiform papillae.

The interpretation of Hincks' plate 25 figure 5 as a depiction of *Cribrilina radiata* var. *α* in the sense of Hincks (1880) is not accepted here. As was noted by Hayward & Ryland (1979), the greater number and different disposition of costae in the figure are clearly at variance with Hincks' written account of the variety. The figure is in fact probably of *Puellina innominata*, an opinion shared by Harmelin (1970:85). Nor is var. *α* considered to be *Puellina setosa* as defined by the lectotype of *P. setosa* chosen above from Waters' material. Rather, Hincks' account is thought to have referred to *Puellina modica* n.sp., with which it agrees closely.

It is not entirely clear whether Hincks regarded the 'vibraculoid setae' as unique to var. *α*. These structures are referred to elsewhere in his (Hincks, 1880) general account of *C. radiata*: p. 186 ('orifice semicircular, . . . on each side of it a very delicate setiform appendage, often wanting') and p. 189 ('The small vibraculoid appendages are often wanting'). They are indeed shown by him in plate 25 figure 2, in the '*innominata* form'. However, Hincks (1883:443) later referred to 'the form which bears vibraculoid setae' in a way which implied that he did consider that these structures characterised a single form or variety within his concept of *C. radiata*. In fact setiform papillae occur throughout the subgenera *Puellina* and *Cribrilaria* as defined above.

Hincks (1880:190) indicated the provenance of his var. *α* material as 'Antrim, deep water (Hyndman)'. No specimen labelled *C. radiata* var. *α* has been found amongst Hincks' material in the BMNH. However, *P. modica* is to be found on a number of shells and stones (bearing other encrusting species and labelled with their names) from Antrim in the Hincks collection (e.g.

BMNH 1899.5.1.1028 and 1899.5.1.1089). In particular, a colony of the species occurred on (but has since been accidentally detached from) a stone encrusted by the cyclostome *Stomatoporina incurvata* (Hincks, 1859) which forms part of the type series (BMNH 1899.5.1.1387) of the cyclostome and is clearly documented as material provided by Hyndman from deep water off Antrim. There seems little doubt that *P. modica* is the form intended by Hincks as *C. radiata* var. *a*.

*Puellina modica* may be distinguished from its close relatives *P. gattyae* and *P. setosa* by its prominent costal ridges. Furthermore, each autozoid has relatively few (typically 5) costae, and the ovicell of *P. modica* has distinct ridges or tubercles whereas those of *P. gattyae* and *P. setosa* are almost smooth.

*P. modica* is also very similar to *P. rarecostata* (Reuss, 1848) from the Badenian (Middle Miocene) of the Vienna Basin (material of *P. rarecostata* examined by SEM: two syntypes, both NMV 1848/38/76; BMNH D55591; all from Eisenstadt). However, *P. rarecostata* has less prominent costal ridges than *P. modica* and a smooth ovicell. The fossil species is in fact intermediate in appearance between *P. modica* and *P. setosa*. It is regarded as a member of the subgenus *Puellina* as defined above.

The occurrence in *P. modica*, *P. bifida* and *P. praecox* n.sp. of ridges or tubercles on the ovicell and of costal ridges that are higher towards the edge of the frontal shield, and the absence of a median umbo in each, impart a similar appearance to these three species. In *P. bifida* and *P. praecox*, however, the exposed gymnocyst is less extensive than in *P. modica*, and the frontal shield more elongate and with more numerous costae. In addition, the oral spine bases are not brown. Unlike *P. modica* and *P. praecox*, *P. bifida* has category A or B ovicells (p. 4).

*P. modica* is known from the English Channel off Sussex, Normandy, Brittany and Guernsey at depths (where known) of 38–106 m; from the Irish Sea; and 'off Antrim' (including material from 'deep water').

#### *Puellina praecox* n.sp.

(Figs 29–35 and Table 5)

Holotype: BMNH 1985.11.20.52e (Channel Stn 248, 49°08.1'N 03°02.3'W, 73 m).

Paratypes (examined by SEM): BMNH: 1911.10.1.1182A (off Antrim); 1936.12.30.335A–C (Liverpool Bay); 1985.11.20.61a (Channel Stn 250); 1985.11.20.72h (Channel Stn 252); D55583 (Red Crag, Plio-Pleistocene, Walton-on-the-Naze, Essex); D55584, D55585, D55586a,b and D55587 (Red Crag, Plio-Pleistocene, Shottisham, Suffolk).

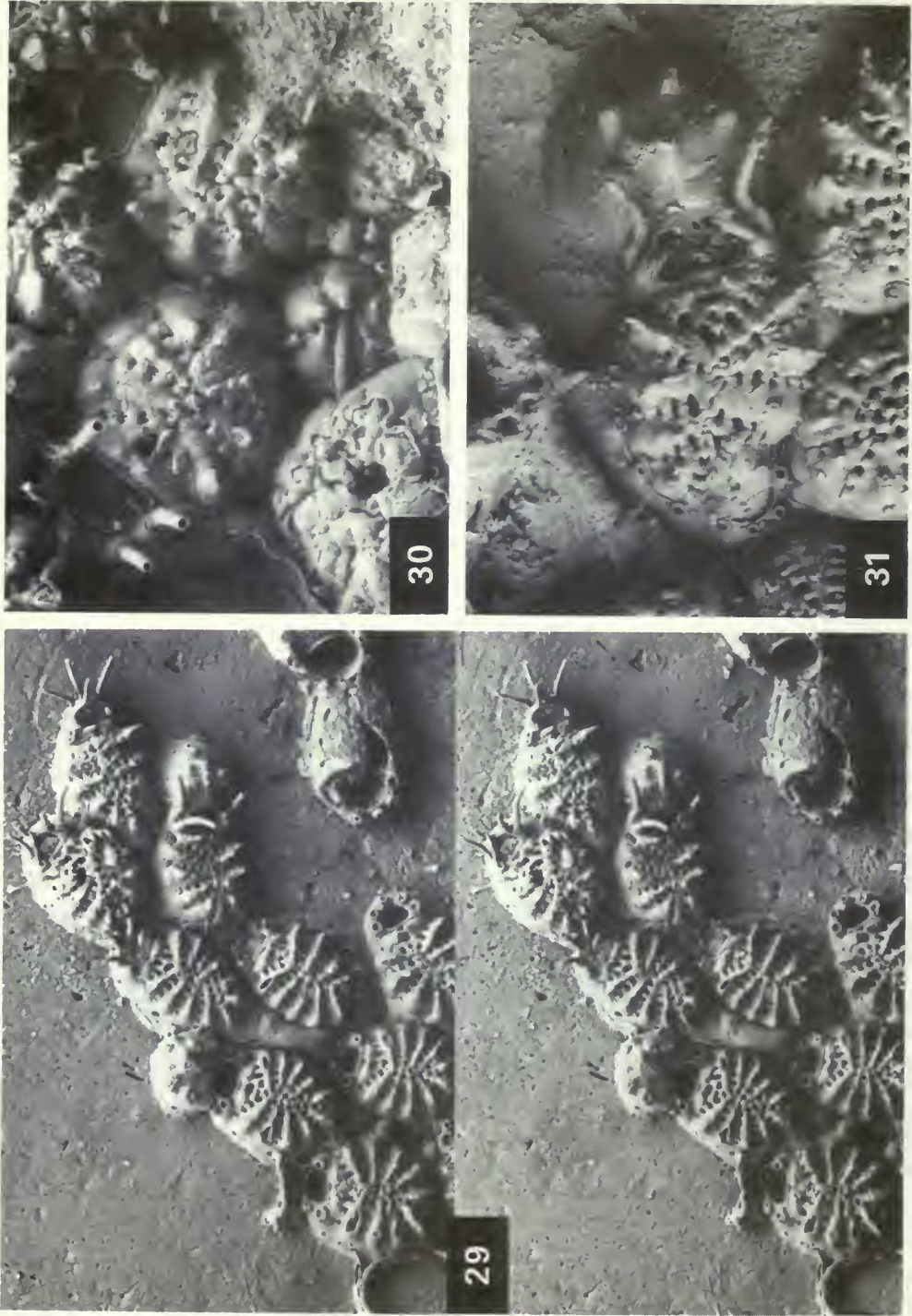
#### OTHER MATERIAL.

BMNH: 1936.12.30.332D (Liverpool Bay); 1936.12.30.333A (no locality [probably Liverpool Bay]); 1985.11.20.91i (Channel Stn 258).

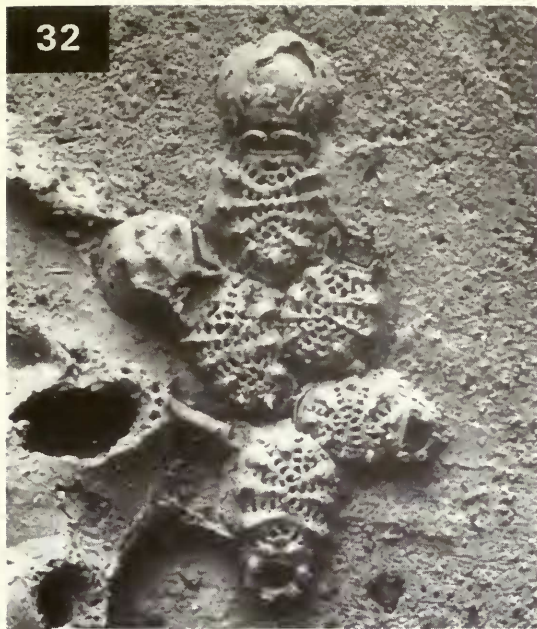
**DESCRIPTION.** Colony encrusting, unilaminar, minute, zooids distinct; largest colonies in available material pluriserial, with only *c.* 20 autozooids. Autozoid generally sub-oval in frontal view (longer than broad). Exposed lateral gymnocyst of autozoid narrow or absent (except at edge of colony); proximal gymnocyst narrow but occasionally with proximal extension(s) between neighbouring zooids.

Frontal shield (= pericyst) lightly calcified, without umbo or any other median thickening; with 8–10 costae each with short, broad, steeply ascending basal portion leading to tapering, nearly horizontal subsequent portion contributing to slightly convex central region of shield. Each costa generally with ridge, decreasing in height gradually from periphery to centre of shield, plus tubercle (occasionally with pelmatidium) near base; degree of development of ridge and tubercle variable. Intercostal pores of variable shape (circular, sub-oval, reniform or sub-rectangular), of variable size throughout shield but often larger in first intercostal row (i.e. just proximal to orifice) than elsewhere, sometimes with denticles adjacent to intercostal suture; 4 (occasionally 3) pores between adjacent costae. Lipped papilla pore between bases of successive costae, about size of adjacent intercostal pore.

Orifice of autozoid D-shaped, slightly broader than long, proximal edge straight. Orifice of ovicellate zooid not appearing truncate in frontal view; width 1.1–1.2 times that of orifice of



**Figs 29–31** *Puellina praecox* n. sp.: (29) stereo pair of holotype (BMNH 1985.11.20.52e), Channel Stn 248,  $\times 75$ ; (30) ancestrula regenerated as kenozooid, with periancestrular non-ovicellate autozooids, BMNH 1985.11.20.61a, Channel Stn 250,  $\times 250$ ; (31) ovicellate autozooid (budded from periancestrular autozooids) part of which occupies zoecium of ancestrula (distal end of ancestrula faces bottom left), BMNH 1936.12.30.335C, Liverpool Bay,  $\times 187$ .



**Figs 32–35** *Puellina praecox* n.sp.: (32) whole colony, BMNH 1936.12.30.335C, Liverpool Bay,  $\times 87$ ; (33) ovicellate autozooid, same specimen,  $\times 210$ ; (34) ancestrula and periancestrular autozooids, BMNH 1936.12.30.335A, Liverpool Bay,  $\times 183$ ; (35) whole colony, BMNH D55586b, Red Crag (Plio-Pleistocene), Shottisham, Suffolk,  $\times 100$ .

**Table 5** *Puellina praecox* n.sp.: measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	44-51	47.3	5.12	11	Lf	169-210	198	6.23	10
b		49-54	51.5	7.73	2		173-219	193	9.46	6
c		—	—	—	0		180	—	—	1
d		40-44	41.7	5.42	3		113-139	128	7.59	7
e		41-45	43.0	7.40	2		168-195	182	11.8	2
f		—	—	—	0		164-189	179	7.27	4
g		38	—	—	1		141-179	163	12.0	4
h		—	—	—	0		137-163	150	13.8	2
a	lo	53-59	56.6	3.83	11	Lfg	203-300	254	12.9	10
b		54-59	56.5	7.04	2		203-301	241	18.8	6
c		—	—	—	0		210	—	—	1
d		47-48	47.5	1.68	2		135-173	162	8.29	7
e		54-57	55.5	4.30	2		217-260	239	14.4	2
f		49-53	51.0	6.24	2		—	—	—	0
g		47	—	—	1		181-231	212	11.8	4
h		—	—	—	0		191-199	195	3.26	2
a	loo	63-72	67.5	10.6	2	lf	143-172	157	6.08	9
b		62-67	64.5	6.17	2		141-166	154	5.81	6
c		65-68	66.5	3.59	2		139-149	144	5.52	2
d		47-55	51.0	12.5	2		97-114	105	7.44	4
e		64	—	—	1		139-148	144	4.98	2
f		—	—	—	0		138-188	156	15.4	4
g		55	—	—	1		145-162	155	5.10	4
h		55	—	—	1		119-134	127	9.44	2
a	Lov	128-148	138	11.6	2	lov	154-167	161	6.45	2
b		130-173	149	12.9	4		160-193	180	9.00	4
c		135-138	137	1.74	2		187-193	190	2.51	2
d		119	—	—	1		124-147	134	9.41	3
e		118	—	—	1		145	—	—	1
f		155	—	—	1		230	—	—	1
g		158	—	—	1		180	—	—	1
h		—	—	—	0		—	—	—	0

a=holotype (BMNH 1985.11.20.52e); b=BMNH 1936.12.30.335A; c=BMNH 1936.12.30.335C; d=BMNH 1985.11.20.61a; e=BMNH 1911.10.1.1182A; f=BMNH D55586a; g=BMNH D55586b; h=BMNH D55584.

non-ovicellate zooid. Oral spines 5 in non-ovicellate zooid, 4 in ovicellate zooid; jointed just above base but without subsequent segmentation, without apophyses. Apertural bar with low tubercle on each side of median suture, and pelmatidium on each tubercle. Median sub-oral lacuna larger than an intercostal pore, of variable shape, occasionally with denticles on proximal margin; occasionally a second lacuna proximal to main lacuna (Fig. 33), smaller than most intercostal pores, denticles not observed.

Each autozooid with *c.* 5 distolateral pore chambers; uncalcified external windows of pore chambers, seen in zooids on edge of colony, relatively small (about the size of an intercostal pore).

Ovicell of category C (p. 4), length 0.7-0.9 times that of frontal shield; frontal surface usually with 2-5 prominent tubercles, sometimes with uncalcified tops.

Kenozooid not present in available material.



Avicularium not present in available material.

Ancestrula (Fig. 34) tatiform, with median proximal spine plus 5 pairs of spines around edge of gymnocyst (i.e. total of 11 spines). Spine morphology unknown. Ancestrula sometimes regenerated as kenozooid (Fig. 30).

ETYMOLOGY. *L. praecox*—ripe before its time, premature, precocious; referring to the development of ovicells early in astogeny in this species.

REMARKS. The dimensions of BMNH 1985.11.20.61a were noticeably smaller than those of the other material measured (Table 5). However, no further differences were noted between this specimen and the others.

*P. praecox* n.sp. closely resembles *P. bifida*, especially in details of the frontal shield (including the apertural bar). However, the frontal shield of *P. praecox* is less heavily calcified than in *P. bifida*, with the costal ridges less well developed. The oral spines of *P. praecox* lack apophyses. The ovicell is of category C (p. 4) (cf. category A or B in *P. bifida*) and typically bears tubercles rather than ridges. The two species may occur at the same locality (Channel Stns 248, 250 and 252) and even on the same shell substrate (BMNH 1985.11.20.52 and 1985.11.20.72).

*Puellina praecox* would be a typical member of the subgenus *Cribrilaria* as defined above but for its category C ovicell. The absence of avicularia may be regarded as a correlate of the small colony size reached by this species.

*P. praecox* is known from the English Channel off Brittany at depths of 73–99 m; from the Irish Sea; from off Antrim; and as a fossil on shells from the Red Crag (Plio-Pleistocene) of Essex and Suffolk (North Sea basin).

***Puellina directa* n.sp.**  
(Figs 36–42 and Table 6).

Holotype: BMNH 1985.11.20.76b (Channel Stn 253, 48°52'2"N 03°54'0"W, 79 m).

Paratypes (examined by SEM): BMNH: 1985.11.20.64e (Channel Stn 250); 1985.11.20.76c,d (Channel Stn 253); 1985.11.20.94d (Channel Stn 258); 1985.11.20.109c and 1985.11.20.110a (Channel Stn 314).

OTHER MATERIAL.

BMNH: 1985.11.20.54f,g (Channel Stn 248); 1985.11.20.56a,b and 1985.11.20.59h (Channel Stn 249); 1985.11.20.62 and 1985.11.20.64f,g (Channel Stn 250); 1985.11.20.65a and 1985.11.20.67b (Channel Stn 251); 1985.11.20.69e,f and 1985.11.20.72i,j (Channel Stn 252); 1985.11.20.83d–f (Channel Stn 256); 1985.11.20.90c,d and 1985.11.20.97b (Channel Stn 258); 1985.11.20.105e–g (Channel Stn 275); 1985.11.20.108g and 1985.11.20.110b (Channel Stn 314).

DESCRIPTION. Colony encrusting, unilaminar, zooids distinct; largest colonies in available material pluriserial to multiserial, with *c.* 100 autozooids. Autozooid of variable shape in frontal view, generally sub-oval (longer than broad). Lateral and proximal gymnocyst of autozooid broad, frequently with short proximal and proximo-lateral extensions between neighbouring zooids.

Frontal shield (= pericyst) moderately to heavily calcified, with little or no differential median thickening, strongly convex, with 7–10 costae (usually 7 or 8). Each costa without clearly differentiated basal and subsequent portions; costal ridge (with narrow longitudinal crest) occupying almost entire length of costa. Most distal two (occasionally three) pairs of costae usually almost parallel, with left and right members of each pair abutting on midline and forming straight line across shield; ridges of these distal costae especially prominent (with crest often irregularly serrate), sometimes continuous from one side of shield to other but more commonly interrupted by narrow V-shaped notch at midline (the latter arrangement especially noticeable when viewed obliquely: Fig. 38). Intercostal pores sub-rectangular or reniform, relatively uniform in size throughout shield, often with denticles adjacent to intercostal suture; usually 3 or 4 pores between successive costae, but frequently fewer between short proximal costae. Lipped papilla pore between bases of successive costae, about same size as, or slightly larger than, an intercostal pore.

Orifice of non-ovicellate autozooid D-shaped, clearly broader than long, proximal edge straight. Orifice of ovicellate zooid not appearing truncate in frontal view; width *c.* 1.3 times that of orifice of

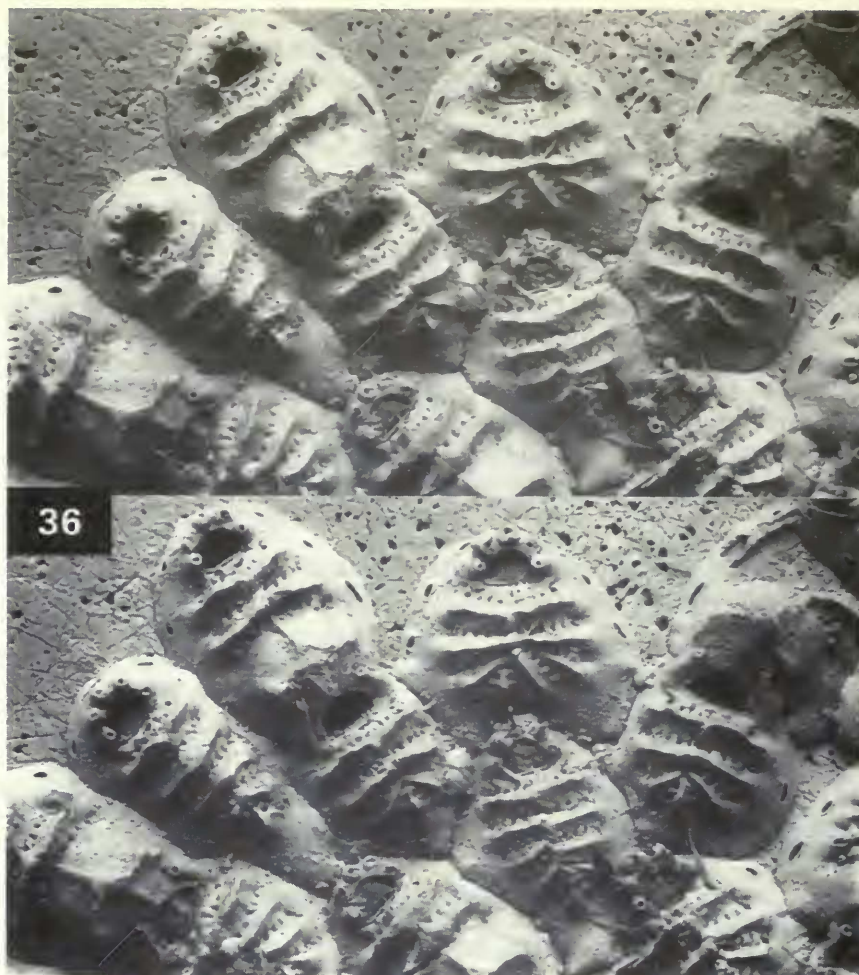


Fig. 36 *Puellina directa* n.sp.: stereo pair of BMNH 1985.11.20.110a, Channel Stn 314,  $\times 103$ .

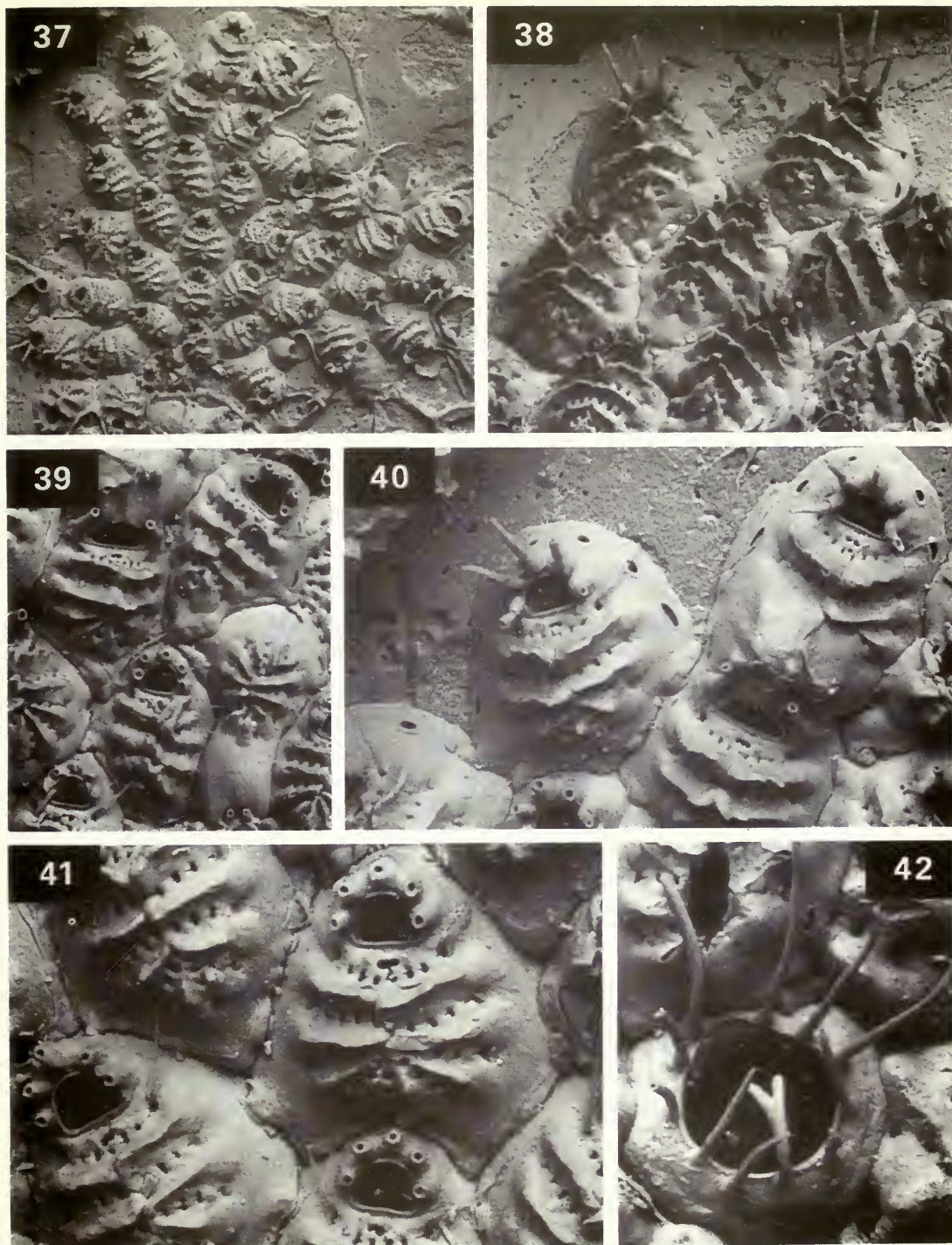
non-ovicellate zooid. Oral spines 5 in non-ovicellate zooid, 2 in ovicellate zooid; jointed some distance above base (Fig. 38), without apophyses. Apertural bar sloping upwards from proximal margin of orifice to first row of intercostal pores; with tubercle each side of median lacuna; minute pelmatidium on each tubercle, and median suture, occasionally discernible. (Pelmatidia not seen elsewhere on shield.) Single median sub-oral lacuna larger than an intercostal pore, frequently with 1 or 2 denticles (which may subdivide lacuna) on proximal margin.

Each autozooid with 5–8 distolateral pore chambers; uncalcified external windows of pore chambers (seen in zooids on edge of colony) of variable size, generally rather small but considerably larger than an intercostal pore.

Ovicell of category A (p. 4), length 0.7–1.1 (usually *c.* 0.9) times that of frontal shield of autozooid; frontal surface non-punctate, generally with median ridge (occasionally with concurrent suture) plus 1 or 2 shorter ridges on each side radiating from median ridge.

Avicularium not present in available material.

Kenozooid (Fig. 39) infrequent, up to size of autozooid, with cribrimorph frontal shield of costae in radiating pattern; gymnocyst broad.



Figs 37–42 *Puellina directa* n.sp.: (37) whole colony, holotype (BMNH 1985.11.20.76b), Channel Stn 253,  $\times 38$ ; (38) edge of colony viewed at angle, holotype,  $\times 95$ ; (39) kenozooid with ovicellate and non-ovicellate autozooids, BMNH 1985.11.20.76c, Channel Stn 253,  $\times 97$ ; (40) ovicellate and non-ovicellate autozooids at edge of colony, holotype,  $\times 129$ ; (41) non-ovicellate autozooid, holotype,  $\times 182$ ; (42) ancestrula, BMNH 1985.11.20.76d, Channel Stn 253,  $\times 240$ .

**Table 6** *Puellina directa* n.sp.: measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	40-48	43.2	7.70	6	Lf	128-162	149	7.19	8
b		43-49	46.0	4.69	7		154-206	175	8.88	9
c		37-48	43.3	6.02	20		131-212	164	11.8	24
a	lo	51-60	55.6	5.88	7	Lfg	173-257	211	12.4	8
b		55-66	60.7	6.21	6		210-294	241	11.2	8
c		58-66	61.0	3.72	20		209-326	241	14.4	23
a	loo	—	—	—	0	lf	117-137	124	5.70	8
b		77-83	79.0	4.76	3		122-148	132	8.40	8
c		75-80	77.0	2.21	9		110-157	135	8.68	29
a	Lov	—	—	—	0	lov	—	—	—	0
b		166	166	0.00	2		225	—	—	1
c		128-157	140	7.37	9		151-198	175	9.47	9

a = holotype (BMNH 1985.11.20.76b); b = BMNH 1985.11.20.76c; c = BMNH 1985.11.20.110a.

Ancestrula (Fig. 42) tatiform, with median proximal spine overarching frontal surface plus 5 pairs of slender erect spines around edge of gymnocyst (i.e. total of 11 spines). Median proximal spine with strongly bifid tip. Spines without apophyses. Regeneration of ancestrula not seen.

ETYMOLOGY. *L. directus*—set straight, arranged in a straight line; referring to the disposition of the more distal pairs of costae in this species.

REMARKS. *P. directa* n.sp. resembles members of the subgenus *Puellina* as defined above (*P. gattya*e, *P. setosa* and *P. modica* n.sp.), except that the ovicell is non-punctate and of category A (p. 4). The species is best characterised by the arrangement of the more distal pairs of costae in parallel or sub-parallel lines right across the strongly convex frontal shield, by the strong costal ridges which tend to be higher towards the centre of the shield, and by the broad gymnocyst which is about as wide laterally as proximally.

*P. directa* is known only from the English Channel off Normandy and Brittany, at depths of 38-99 m.

***Puellina (Cribrilaria) venusta* Canu & Bassler, 1925**  
(Figs 43-49, 99 and Table 7)

part *Cribrilaria radiata*, *radiata* form: Hincks, 1880; 185-190, pl. 25 figs 3, 76.

*Puellina venusta* Canu & Bassler, 1925; 22, pl. 2 fig. 5.

*Cribrilaria crenulata* Harmelin, 1970; 91-93, fig. li-k, pl. 2 figs 1-3.

*Cribrilaria venusta*: Harmelin, 1978; 180, 182, 184, pl. 2 figs 3-5.

*Cribrilaria venusta*: Hayward & Ryland, 1978; 146.

part or whole *Cribrilaria radiata*: Hayward & Ryland, 1979; 62, 63, fig. 16A,B.

*Cribrilaria venusta*: Hayward & Cook, 1983; 43, 45, fig. 11A.

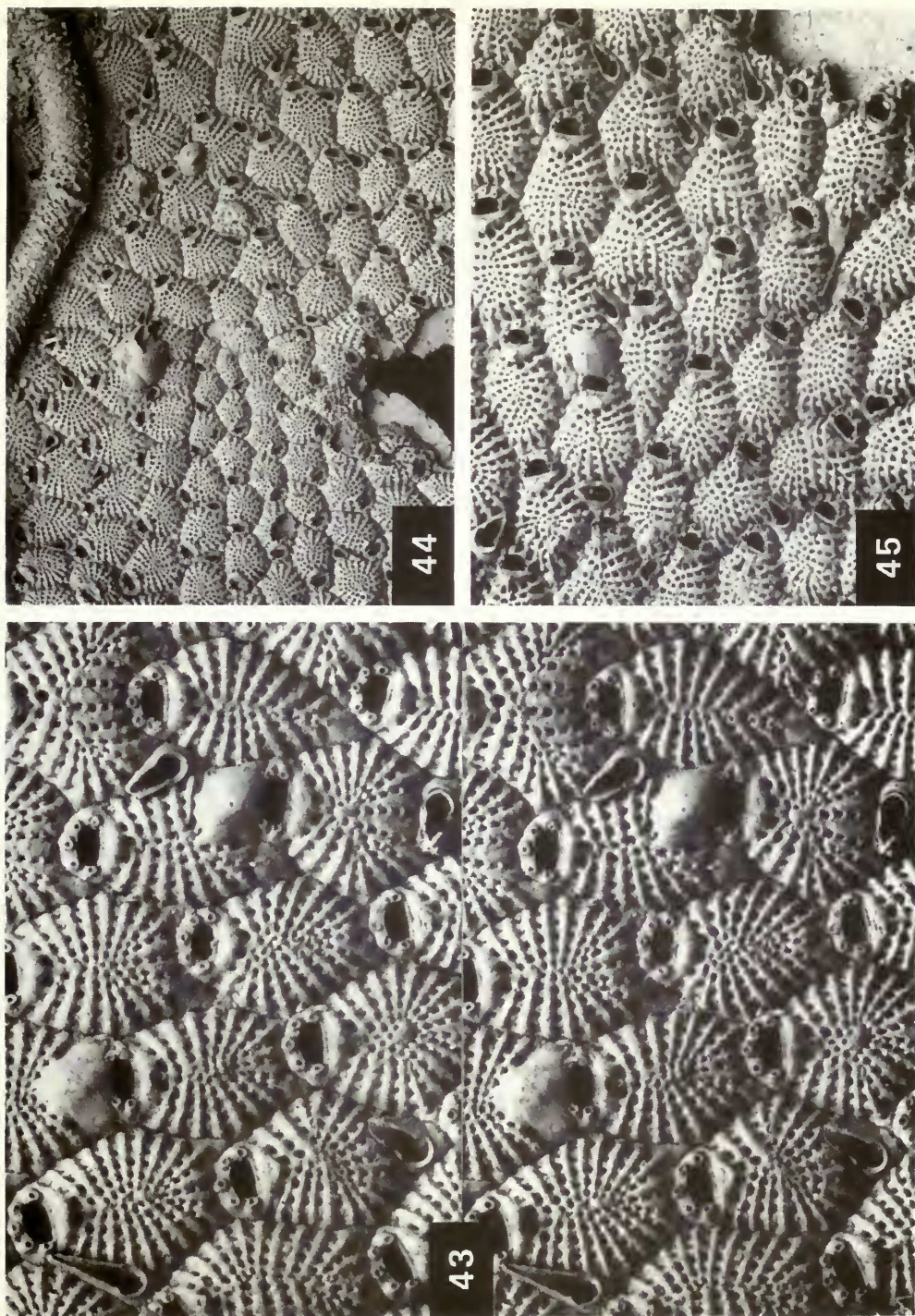
**MATERIAL EXAMINED BY SEM.**

BMNH: 1911.10.1.711 (Fosse de Cap Breton); 1985.11.20.68 (Channel Stn 252); 1985.11.20.82a (Channel Stn 256); 1985.11.20.117 (Channel Stn 318); D55588 (Badenian, Hartl-lucke, Eisenstadt).

LBIMM: BRY-6527 (Marseille, holotype of *Cribrilaria crenulata* Harmelin, 1970).

**OTHER MATERIAL.**

Holotype: IP, Canu Collection (no registration number) (34°12'N, 07°07'W, off Rabat, Morocco, 140-150 m).



Figs 43–45 *Puellina venusta* Canu & Bassler, BMNH 1985.11.20.82a, Channel Stn 256: (43) stereo pair,  $\times 63$ ; (44) colony origin and early generations of autozooids (all non-ovicellate),  $\times 25$ ; (45) part of colony viewed at angle.  $\times 44$ .

BMNH: 1911.10.1.706 (Guernsey, two colonies on separate substrates); 1911.10.1.712 (Birturbuy [= Bertraghboy] Bay [Galway]); 1911.10.1.732 (Shetland, 320 m, colony and substrate, a pebble, broken in two); 1919.6.24.39 (Guernsey); 1985.1.2.54, 1985.1.2.83 and 1985.1.2.88 (northern Bay of Biscay); 1985.11.20.83b (Channel Stn 256); 1985.11.20.87b (Channel Stn 257); 1985.11.20.103b,c (Channel Stn 261); 1985.11.20.104c, d (Channel Stn 263); 1985.11.20.113 (Channel Stn 316).

**DESCRIPTION.** Colony encrusting, unilaminar, zooids distinct; largest colonies in available material multiserial, with well over 1000 autozooids. Autozoid of very variable shape in frontal view, generally sub-oval but commonly broadly bifid proximally (when passing to both sides of proximal zoid) or elongate. Exposed lateral and proximal gymnocyst of autozoid very narrow or absent (except at edge of colony), but frequently with short proximal extension(s) between neighbouring zooids.

Frontal shield (= pericyst) lightly to moderately calcified, without median thickening (except on apertural bar—see below), with 12–23 costae (most commonly 15–18; high numbers generally occurring in proximally bifid zooids, in which the pattern of costae may be partially duplicated, or in elongate zooids). Each costa with short, steeply ascending basal portion leading to tapering, nearly horizontal subsequent portion contributing to slightly convex central region of shield; without ornamentation; up to 3 minute pematidia along length of each costa. Intercostal pores sub-oval, of variable size throughout shield but generally slightly larger in row immediately proximal to apertural bar than in rest of shield, without denticles; 3 or 4 pores between successive costae. Lipped papilla pore between bases of successive costae, about size of adjacent intercostal pore.

Orifice of non-ovicellate autozoid D-shaped, very clearly broader than long, proximal edge straight or indistinctly crenulate. Orifice of ovicellate zoid frequently appearing distally truncate to varying extent in frontal view because of overhanging calcification of ovicell; width 1.0–1.1 times that of orifice of non-ovicellate zoid. Oral spines 5 in non-ovicellate zoid, 4 in ovicellate zoid; jointed just above base, with adjacent constriction (Fig. 47); apophyses not seen. Apertural bar forming short triangular area, sloping steeply upwards from proximal margin of orifice to form median sub-oral mucro; mucro of variable development, sometimes spiniform or bifid; apertural bar without tubercles; pematidia and median suture not seen. Without median sub-oral lacuna.

Each autozoid with about 9 distolateral pore chambers; uncalcified external windows of pore chambers, seen in zooids on edge of colony (Fig. 48), often sub-rectangular, very large (much larger than an intercostal pore).

Ovicell of category A (p. 4), with rather variable outline in frontal view, length 0.5–0.6 times that of frontal shield of autozoid; frontal surface non-punctate, with variably developed median or diagonal ridge, sometimes with concurrent suture.

Avicularium frequent, interzooidal, smaller than autozoid; palate elongate-triangular, inclined at low angle to substrate; rostrum generally directed between autozooids. Mandible equal in length to palate and of same shape, i.e. fitting into palate. Proximal gymnocyst short (much shorter than palate plus frontal non-calcified area).

Kenozooid (Fig. 48) infrequent, up to size of autozoid, with cribrimorph frontal shield of costae in radiating pattern.

Ancestrula (Fig. 49) tatiform, with median proximal spine plus 5 pairs of spines around edge of gymnocyst (i.e. total of 11 spines). Details of segmentation (if any) of spines not seen. Morphology of median proximal spine not seen. Other spines each with upwardly directed spiniform apophysis on inner surface near base. Regeneration of ancestrula not seen.

---

**Figs 46–49** *Puellina venusta* Canu & Bassler: (46) ovicellate and non-ovicellate autozooids and avicularium, BMNH 1985.11.20.82a, Channel Stn 256,  $\times 116$ ; (47) non-ovicellate autozooids (some with basal portions of oral spines intact) and avicularia (with mandibles intact), BMNH 1985.11.20.68, Channel Stn 252,  $\times 145$ ; (48) edge of colony, maternal autozoid (top left) arrowed, BMNH 1911.10.1.711, Fosse de Cap Breton,  $\times 49$ ; (49) ancestrula, BMNH 1985.11.20.117, Channel Stn 318,  $\times 230$ .

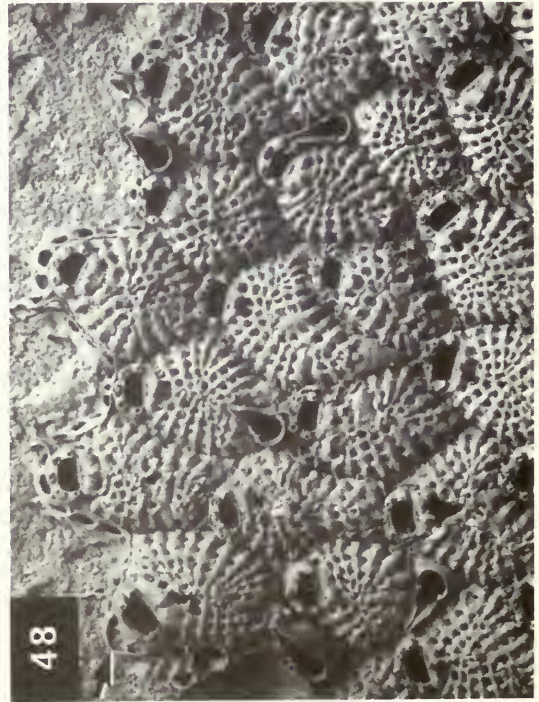


Table 7 *Puellina venusta* Canu & Bassler: measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	48-57	53.5	6.83	6	Lf	277-345	302	6.72	9
b		51-61	57.9	5.91	8		256-350	306	9.20	9
c		49-65	57.0	6.59	26		283-372	326	7.42	29
d		53-71	60.9	10.7	7		274-378	317	12.4	6
a	lo	80-95	85.1	6.64	7	Lfg	342-445	371	8.85	9
b		77-100	86.7	8.27	10		281-433	343	13.0	10
c		81-100	91.5	4.68	25		353-486	413	9.42	27
d		82-94	87.3	6.19	7		352-444	386	11.7	5
a	loo	87-94	90.3	4.21	3	lf	244-322	267	8.79	10
b		87	—	—	1		169-336	253	21.4	11
c		97	—	—	1		254-406	304	13.0	18
d		82-94	86.8	6.43	4		219-279	247	9.23	9
a	Lov	141-167	153	7.68	4	Lr	187-209	198	8.84	2
b		147	—	—	1		156	—	—	1
c		158-170	164	5.82	2		160-230	180	16.5	5
d		167-197	179	8.29	4		195-203	199	2.18	3
a	lov	152-168	163	6.15	3	Lav	220-241	231	7.25	2
b		155	—	—	1		233	—	—	1
c		184-228	206	17.0	2		183-284	221	18.4	5
d		195-213	207	4.37	4		220-245	231	6.06	3

a=BMNH 1911.10.1.711; b=BMNH 1985.11.20.68; c=BMNH 1985.11.20.82a; d=LBIMM-BRY-6527 (holotype of *Cribrilaria crenulata* Harmelin).

REMARKS. In a taxonomic account of Mediterranean species referred to *Cribrilaria*, Harmelin (1970) redescribed *C. radiata* (Moll, 1803), of which a neotype was designated, and described as new a species to which he gave the name *C. crenulata*. *C. crenulata* was later realised (Harmelin, 1978) to be a geographical variant of the formerly overlooked species *Puellina venusta* Canu & Bassler, 1925, which had been described from the Atlantic off Morocco. The two forms *P. radiata* and *P. venusta* seem to be very closely related. *P. radiata*, as defined by the neotype, is thought to be restricted to the Mediterranean (Harmelin, 1978:174 and pers. comm. to JDDDB, 1985), although the name has been widely applied to Atlantic material referable to *P. venusta*.

Traces of the crenulate proximal margin of the orifice shown by Mediterranean specimens described as *Cribrilaria crenulata* by Harmelin (1970) may be seen, albeit indistinctly, in some Atlantic material (BMNH 1911.10.1.711). As noted by Harmelin (1970), avicularia in Recent Mediterranean material frequently show multiple regenerations stacked one on top of the other; this was also reported in Atlantic material studied by Harmelin (1978) and Aristegui (1983). Autozooids of the holotype of *C. crenulata* have up to 12 distolateral pore chambers. Harmelin (1978:180) stated that oral spines of *P. venusta* sometimes have 'une couronne de spinules légèrement au-dessus de leur base'. The median proximal spine of the ancestrula of material studied by Harmelin (1970:92 and fig. 3b) has a bifid tip.

The specimen figured by Hayward & Ryland (1979: fig. 16A,B, as *Cribrilaria radiata*) is BMNH 1911.10.1.711 (Fig. 48). Part of the material studied by Hayward & Ryland (1978) is in the BMNH collections (1985.1.2.54, 1985.1.2.83 and 1985.1.2.88).



*P. venusta* is a common fossil species encrusting shells from the Badenian (Middle Miocene) of Eisenstadt in the Vienna Basin. The fossil (Fig. 99) has slightly more extensive gymnocyst than has most Recent material (Figs 43–49), but agreement is otherwise close. The Badenian of Eisenstadt is the type locality of a very similar species, *Puellina scripta* (Reuss, 1848). The holotype of *P. scripta*, NMV 1848/38/75, is illustrated in Figure 98, and is the only colony of the species examined. In this specimen the avicularium is consistently larger than in *P. venusta*, the sub-oral mucro of the autozoid is poorly developed or absent, and the frontal shield almost flat. *P. scripta* is therefore very close to the Recent Mediterranean species *P. radiata*. It differs only in the presence of 5 oral spines in all non-ovicellate autozooids whereas in *P. radiata* the usual complement is 4 spines, with 20–60% of zooids in rare colonies having 5 (Harmelin, 1970). The name *P. scripta* has been placed in synonymy with *P. radiata* by several authors, although it has been applied at least once to Recent material (Manzoni, 1871). It is interesting to note that the co-occurrence of the apparently closely related entities *P. venusta* and *P. scripta*/*P. radiata* in the Paratethys during Middle Miocene times persists to the present day in the Mediterranean. The taxonomic status of these forms requires clarification.

In the English Channel material studied in the present paper, *P. venusta* occurred off Brittany at depths of 82–102 m. It was reported at greater depths (180–182 m and 250–270 m) in the northern Bay of Biscay by Hayward & Ryland (1978). *P. venusta* appears to have a wide present-day latitudinal range. The most northerly material available is from deep water (320 m) off the Shetlands (BMNH 1911.10.1.732). The species was described originally from material collected off Rabat (Morocco), and has been recorded from the Canaries by Aristegui (1983; 1984) and off the eastern coast of South Africa at a depth of 90 m by Hayward & Cook (1983).

***Puellina (Cribrilaria) innominata* (Couch, 1844)**  
(Figs 50–58 and Table 8)

*Lepralia innominata* Couch, 1844; 114, 115, pl. 22 fig. 4.

*Lepralia innominata*: Johnston, 1847; 319, 320, pl. 55 fig. 12.

not *Lepralia innominata*: Busk, 1859; 40, pl. 4 fig. 2.

part or whole *Cribrilaria radiata*, *innominata* form: Hincks, 1880; 185–190, pl. 25 figs 1, 2, 5.

*Cribrilaria innominata*: Hayward & Ryland, 1979; 64, fig. 17A–D.

*Cribrilaria innominata*: Bishop, 1986; 96, 98, figs 1–8.

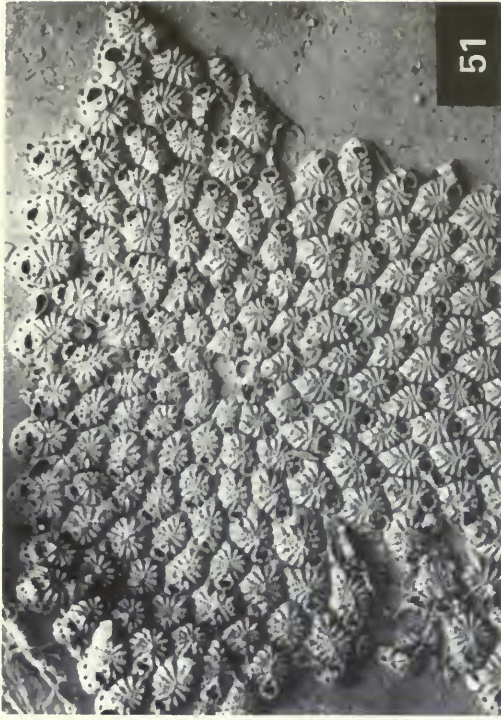
**MATERIAL EXAMINED BY SEM.**

Neotype: 1847.9.16.32 (Goran [Cornwall]; selected by Bishop, 1986).

BMNH: 1897.5.1.632 (Hastings); 1899.5.1.720A (British); 1899.5.1.723 (Antrim); 1911.10.1.723 (British); 1936.12.30.335B (Liverpool Bay); 1985.11.20.41b (off Craggan Rocks, S. Cornwall); 1985.11.20.73a and 1985.11.20.76a (Channel Stn 253); 1985.11.20.102a (Channel Stn 260); 1985.11.20.103d (Channel Stn 261); 1985.11.20.116b (Channel Stn 318).

**OTHER MATERIAL.**

BMNH: 1847.9.16.53 (British); 1847.9.16.122 (Sana Island [W. Scotland]); 1847.9.16.161 (British, colony numbered 2); 1847.9.16.162 and 1899.5.1.720B, D (British); 1899.5.1.722 (Guernsey, colonies on three shells); 1911.10.1.720 and 1911.10.1.721 (British, numerous colonies on shell fragments); 1911.10.1.722 (Shetland, several colonies on pebbles); 1911.10.1.725 (Guernsey, several colonies on shell fragments); 1911.10.1.726 (Birturbuy [= Bertraghboy] Bay [Galway]), numerous colonies on shell fragments); 1919.6.24.35 (Birturbuy [= Bertraghboy] Bay [Galway]); 1936.12.30.332A–D (Liverpool Bay); 1936.12.30.333A–J and 1936.12.30.334 (no locality [probably Liverpool Bay]); 1936.12.30.335C (Liverpool Bay); 1963.3.30.142 (Plymouth, several colonies); 1985.11.20.42a–c, 1985.11.20.43 and 1985.11.20.44a–i (off Craggan Rocks, S. Cornwall); 1985.11.20.67a (Channel Stn 251); 1985.11.20.69d, 1985.11.20.70a and 1985.11.20.72e,f (Channel Stn 252); 1985.11.20.74d and 1985.11.20.81a (Channel Stn 253); 1985.11.20.83c (Channel Stn 256); 1985.11.20.88a,b (Channel Stn 257); 1985.11.20.91b and 1985.11.20.98b (Channel Stn 258); 1985.11.20.102b (Channel Stn 260); 1985.11.20.103e (Channel Stn 261); 1985.11.20.104e–h (Channel Stn 263); 1985.11.20.105d and 1985.11.20.107c (Channel Stn 275); 1985.11.20.111a and 1985.11.20.112a (Channel Stn 315); 1985.11.20.116c–k (Channel Stn 318).



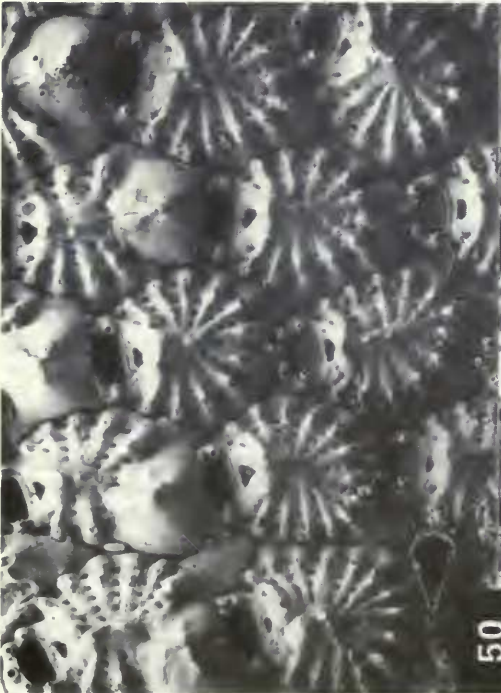
51



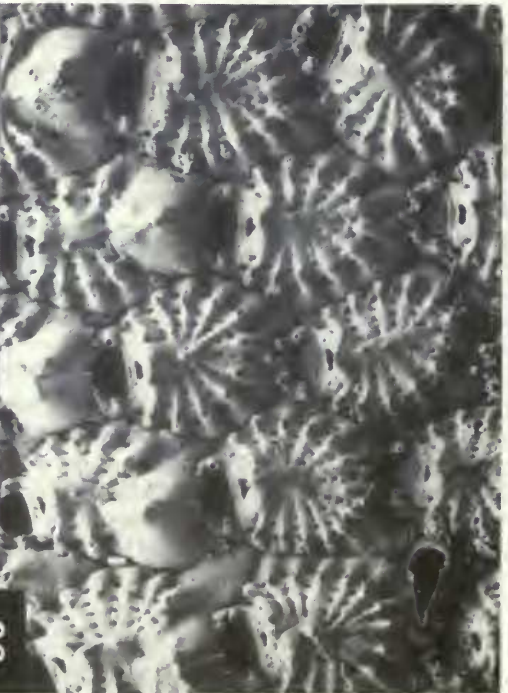
53



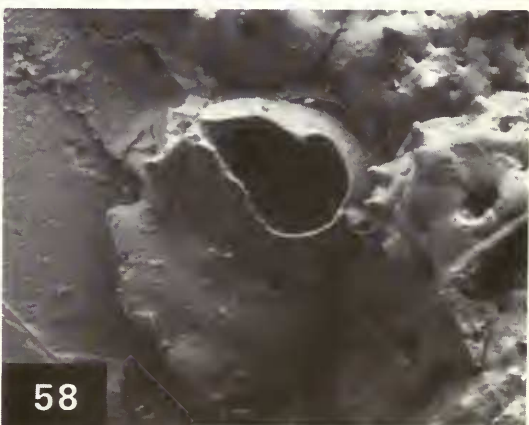
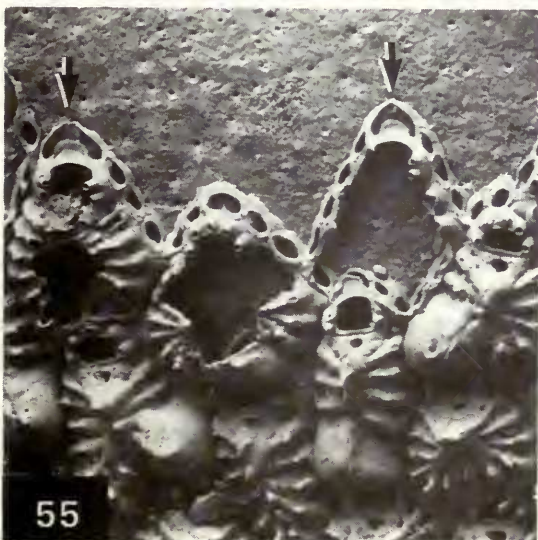
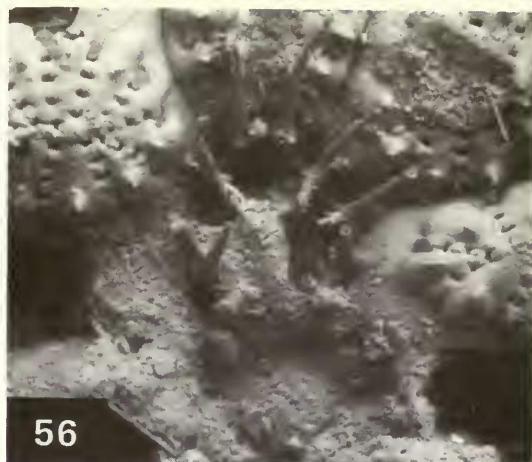
52



50



Figs 50-53 *Puellina innominata* (Couch): (50) stereo pair of BMNH 1899.5.1.720A, British,  $\times 69$ ; (51) part of colony, BMNH 1911.10.1.723, British,  $\times 16$ ; (52) avicularium, BMNH 1897.5.1.632, Hastings,  $\times 142$ ; (53) avicularium, same colony,  $\times 131$ .



**Figs 54–58** *Puellina innominata* (Couch): (54) non-ovicellate autozoid, BMNH 1899.5.1.720A, British,  $\times 143$ ; (55) edge of colony with abraded autozooids, arrows indicate maternal autozooids, same specimen,  $\times 58$ ; (56) ancestrula (partially obscured), BMNH 1985.11.20.102a, Channel Stn 260,  $\times 164$ ; (57) ancestrula regenerated as kenozooid (note bifid top of median proximal spine of ancestrula), BMNH 1985.11.20.116b, Channel Stn 318,  $\times 280$ ; (58) ancestrula regenerated as avicularium, BMNH 1985.11.20.73a, Channel Stn 253,  $\times 200$ .

DESCRIPTION. Colony encrusting, unilaminar, zooids distinct; largest colonies in available material multiserial, with well over 1000 autozooids. Autozooid of variable shape in frontal view, generally sub-oval (longer than broad) but occasionally broadly bifid proximally when passing to both sides of proximal zooid. Exposed lateral gymnocyst of autozooid narrow or absent (except at edge of colony); proximal gymnocyst narrow or of moderate width, frequently with proximal extension(s) between neighbouring zooids.

Frontal shield (= pericyst) moderately to heavily calcified, with 9–14 costae (most commonly 11 or 12; sometimes more than 14 in proximally bifid zooids in which pattern of costae is partially duplicated), with prominent distal median umbo and variable median ridge proximal to umbo. Each costa with short, broad, steeply ascending basal portion (sometimes seen to bear minute pelmatidium) leading to tapering, nearly horizontal subsequent portion contributing to slightly

**Table 8** *Puellina innominata* (Couch): measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	47–55	50.1	4.87	11	Lf	216–294	254	7.67	13
b		57–63	58.9	3.08	12		238–291	268	6.09	17
c		—	—	—	0		219–284	247	8.32	12
d		55–60	57.0	3.41	11		284–369	323	8.77	11
e		56	—	—	1		293–338	308	7.01	4
f		51–62	56.5	6.01	10		250–308	278	6.33	11
a	lo	79–89	83.7	3.78	11	Lfg	293–439	363	12.8	13
b		81–89	85.3	2.72	12		325–454	369	10.7	13
c		74–92	81.8	6.17	11		311–448	363	13.2	11
d		88–103	96.0	4.58	10		404–508	455	8.53	10
e		88–95	92.3	4.44	3		384–449	406	10.0	3
f		81–90	86.3	3.27	10		325–433	384	10.7	9
a	loo	89–94	91.0	3.15	3	lf	188–266	223	8.85	13
b		91–100	97.1	4.69	8		203–265	229	7.35	18
c		74–86	80.0	11.9	2		184–272	220	13.0	15
d		96–112	105	7.00	4		231–300	266	8.26	15
e		95–115	101	10.3	4		221–268	234	6.86	8
f		91–97	94.0	3.46	3		216–298	251	10.5	11
a	Lov	172–177	175	2.28	2	Lr	174–178	176	1.81	2
b		170–188	181	3.12	8		164	—	—	1
c		145–174	162	10.2	3		—	—	—	0
d		191–238	208	9.28	6		230–234	232	1.37	2
e		163–233	195	17.6	4		—	—	—	0
f		181–195	188	3.23	4		—	—	—	0
a	lov	213	—	—	1	Lav	260–267	264	2.12	2
b		195–206	200	2.00	7		180	—	—	1
c		184–229	203	12.5	3		—	—	—	0
d		192–254	229	10.4	6		318–326	322	1.98	2
e		166–214	192	13.7	3		—	—	—	0
f		201–231	215	6.29	4		—	—	—	0

a = neotype (BMNH 1847.9.16.32); b = BMNH 1899.5.1.720A; c = BMNH 1899.5.1.723; d = BMNH 1911.10.1.723; e = BMNH 1985.11.20.103d; f = BMNH 1985.11.20.76a.

convex central region of shield; tubercle or short ridge at junction of the two portions of each costa, near periphery of shield. Intercostal pores of variable shape (round, sub-oval, reniform or sub-rectangular), of relatively uniform size throughout shield, sometimes with denticles adjacent to intercostal suture; 1–5 (most commonly 3 or 4) pores between successive costae. Lipped papilla pore between bases of successive costae, considerably larger than adjacent intercostal pore.

Orifice of non-ovicellate autozoid D-shaped, very clearly broader than long, proximal edge straight. Orifice of ovicellate zoid frequently appearing distally truncate to variable extent in frontal view because of overhanging calcification of ovicell; width 1.0–1.1 times that of orifice of non-ovicellate zoid. Oral spines 5 in non-ovicellate zoid, 4 in ovicellate zoid; jointed just above base; with inwardly directed, inconspicuous half-circle of denticles near base. Apertural bar forming triangular area, sloping upwards from proximal margin of orifice to umbo; with minute palmatidium each side of indistinct median suture; without tubercles. Single, very large median sub-oral lacuna (much larger than an intercostal pore), variable in shape but frequently sub-triangular, with base of triangle towards orifice; without denticles.

Each autozoid with 7–9 distolateral pore chambers; uncalcified external windows of pore chambers (seen in zooids on edge of colony: Fig. 55) relatively large (as large as or larger than sub-oral lacuna).

Ovicell of category A (p. 4), length generally 0.6–0.7 times that of frontal shield of autozoid; frontal surface non-punctate, with up to 4 indistinct tubercles or short ridges in more or less radiating pattern, occasionally approximating to central umbo; frequently with median suture.

Avicularium (Figs 52, 53) infrequent to fairly frequent, interzooidal, considerably smaller than autozoid. Palate elongate-triangular, inclined at moderate angle to substrate (highest distally); rostrum generally directed between autozooids. Mandible equal in length to palate and of same shape, fitting into it. Length of proximal gymnocyst of avicularium clearly shorter than that of palate plus frontal non-calcified area. Frontal non-calcified area sometimes occupied by cribrimorph frontal shield after regeneration as kenozooid.

Kenozooid infrequent (BMNH 1985.11.20.103d only), slightly smaller than autozoid, with cribrimorph frontal shield of costae in radiating pattern; gymnocyst narrow.

Ancestrula (Fig. 56) tatiform, with median proximal spine overarching frontal surface plus 5 pairs of erect spines around edge of gymnocyst (i.e. total of 11 spines). Details of jointing (if any) of spines not seen. Median proximal spine with strongly bifid tip (Fig. 57). Most distal pair of spines each with short, minutely denticulate, inwardly directed apophysis near base. Remaining eight erect spines each with inwardly directed spiniform apophysis (sometimes with lateral denticles and minutely bifid tip) near base. Ancestrula sometimes regenerated as kenozooid (Fig. 57), or rarely as avicularium (BMNH 1985.11.20.73a: Fig. 58).

REMARKS. The identity of *Puellina innominata* has been discussed, and a neotype selected, by Bishop (1986). The species is generally well characterised around the British Isles, where variation is largely limited to the degree of development of the costal ridges and umbo. However, many other forms apparently related to *P. innominata* as defined by the neotype are known from other parts of the world, and the elucidation of the status of these would involve an immense amount of study.

Material from the British Isles and adjacent waters studied in the present paper was collected from the English Channel off Sussex, Normandy, Brittany, Guernsey, Devon and Cornwall (depths, where known, 38–106 m); from Galway; from the Irish Sea; off Antrim; off the W. coast of Scotland; and from the Shetlands.

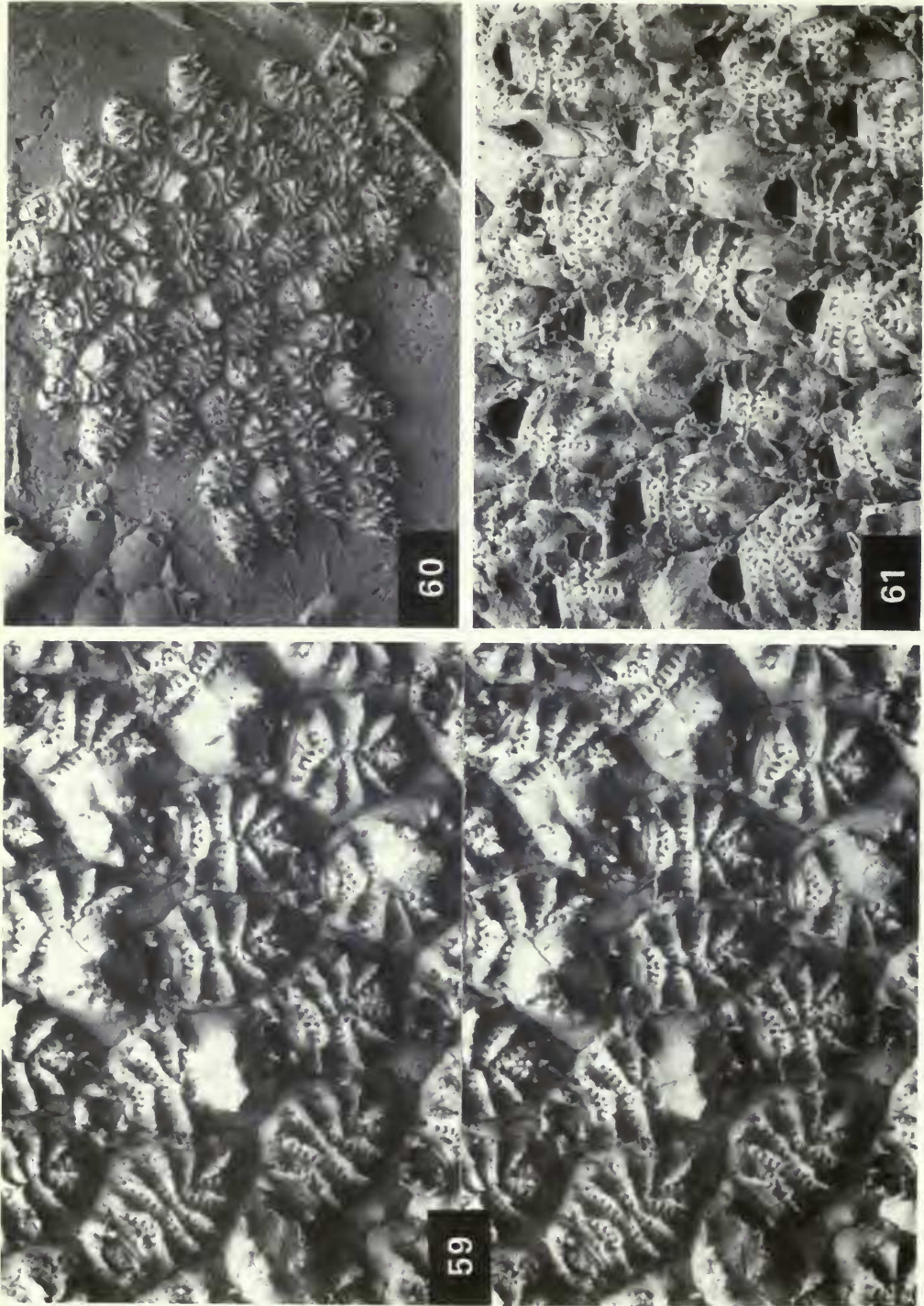
***Puellina (Cribrilaria) bifida* (d'Hondt, 1970)**  
(Figs 59–72 and Table 9)

*Colletosia innominata* subsp. *bifida* d'Hondt, 1970; 246–248, fig. 12a-c.

MATERIAL EXAMINED BY SEM.

Lectotype (selected here); LBIMM-BRY-11603 (48°01'N, 05°44'W, 130 m).

BMNH: 1911.10.1.735B (Belfast); 1911.10.1.1182B (off Antrim); 1936.12.30.331A (two colonies) and B (no locality [probably Liverpool Bay]); 1985.11.20.41a (off Craggan Rocks, S. Cornwall); 1985.11.20.71a and 1985.11.20.72d (Channel Stn 252); 1985.11.20.94b, c (Channel Stn 258); 1985.11.20.103a (Channel Stn 261).



Figs 59-61 *Puellina bifida* (d'Hondt): (59) stereo pair of lectotype (LBIM-BRY-11063), off Finistère,  $\times 83$ ; (60) whole colony, lectotype,  $\times 30$ ; (61) part of colony viewed at angle, BMNH 1936.12.30.331B, no locality,  $\times c. 70$ .

## OTHER MATERIAL.

BMNH: 1847.9.16.161 (British, colony numbered 1); 1899.5.1.720C (British); 1899.5.1.953 (Antrim); 1911.10.1.731 (British); 1911.10.1.737B (Guernsey); 1936.12.30.331C,D (no locality [probably Liverpool Bay]); 1936.12.30.332B and 1936.12.30.335C (Liverpool Bay); 1985.11.20.45 (Channel Stn 183); 1985.11.20.47 (Channel Stn 240); 1985.11.20.52b-d, 1985.11.20.53 and 1985.11.20.54a-e (Channel Stn 248); 1985.11.20.57a and 1985.11.20.59b-f (Channel Stn 249); 1985.11.20.60a, 1985.11.20.63a and 1985.11.20.64a-d (Channel Stn 250); 1985.11.20.69b,c (Channel Stn 252); 1985.11.20.74c and 1985.11.20.77a, b (Channel Stn 253); 1985.11.20.83a (Channel Stn 256); 1985.11.20.87a and 1985.11.20.89 (Channel Stn 257); 1985.11.20.90a,b, 1985.11.20.91a, 1985.11.20.92a, 1985.11.20.93a, 1985.11.20.94a, 1985.11.20.96a, 1985.11.20.97a and 1985.11.20.98a (Channel Stn 258); 1985.11.20.104a,b (Channel Stn 263); 1985.11.20.105a-c and 1985.11.20.107a,b (Channel Stn 275); 1985.11.20.108b-d and 1985.11.20.109b (Channel Stn 314); 1985.11.20.111b (Channel Stn 315); 1985.11.20.114 (Channel Stn 317); 1985.11.20.116a (Channel Stn 318).

**DESCRIPTION.** Colony encrusting, unilaminar, zooids distinct; largest colonies in available material pluriserial to multiserial, with over 200 autozooids. Autozoid of variable shape in frontal view, generally sub-oval (longer than broad). Lateral and proximal gymnocyst of autozoid narrow or of moderate width, but frequently with proximal and proximo-lateral extensions between neighbouring zooids.

Frontal shield (=pericyst) of autozoid moderately calcified, with little or no differential median thickening and no umbo, with 6–11 costae (usually 7–9). Each costa with short, broad, steeply ascending basal portion at periphery of frontal shield leading to tapering, nearly horizontal subsequent portion contributing to almost flat central region of shield. Costal ridges prominent, raised near edge of shield but lower centrally, frequently showing abrupt decrease in height between periphery and centre of shield giving characteristic appearance (especially noticeable when viewed obliquely: Fig. 61). Intercostal pores sub-rectangular or reniform, relatively uniform in size throughout shield, often with denticles adjacent to intercostal suture; usually 4, occasionally 5, pores between successive costae, but frequently fewer between short proximal costae. Lipped papilla pore between bases of successive costae, about size of adjacent intercostal pore.

Orifice of non-ovicellate autozoid D-shaped, clearly broader than long, proximal edge straight. Orifice of ovicellate zooid frequently appearing distally truncate to varying extent in frontal view because of overhanging calcification of ovicell; width 1.1–1.2 times that of orifice of non-ovicellate zooid. Oral spines 5 in non-ovicellate zooid, 4 in ovicellate zooid; jointed at base and generally with inwardly directed spiniform apophysis near base. Apertural bar with low tubercle each side of median suture and pematidium on each tubercle. (Pematidia not observed elsewhere on shield.) Single median sub-oral lacuna between tubercles of apertural bar and first row of intercostal pores, about same size as an intercostal pore, frequently with pair of denticles on proximal margin; lacuna occasionally confluent with adjacent intercostal pores.

Each autozoid with 5–8 distolateral pore chambers; uncalcified external windows of pore chambers, seen in zooids on edge of colony (Fig. 67), relatively large (considerably larger than an intercostal pore).

Ovicell of category A or occasionally B (p. 4) (Fig. 70), length 0.7–0.9 times that of frontal shield of autozoid; frontal surface non-punctate, frequently with up to 4 ridges in more or less radiating pattern, with median suture.

Avicularium absent in holotype, infrequent in other material (Figs 65–67), interzooidal, smaller than an autozoid, nearly always seen on periphery of colony (exceptions occurring at sites of apparent disruption to colony growth in BMNH 1936.12.30.331A). Palate elongate-triangular, of somewhat variable length, often curving down towards substrate distally. Mandible elongate-triangular, sometimes with very acute tip produced beyond (? damaged or incomplete) palate as narrow down-curved extension (seen in dried material). Cystid of avicularium with 2 or 3 pore chamber windows; length of proximal gymnocyst about equal to that of palate plus frontal non-calcified area. Frontal non-calcified area sometimes occupied by cribrimorph frontal shield after regeneration as kenozooid (Fig. 69).

Kenozooid (Fig. 68) infrequent, generally smaller than an autozoid, with cribrimorph frontal shield of costae in radiating pattern.

Ancestrula (Fig. 71) tatiform, with median proximal spine overarchng frontal surface plus 5 pairs of erect spines around edge of gymnocyst (i.e. total of 11 spines). Erect spines jointed at base and with at least 2 subsequent segments. Median proximal spine with broad, sometimes slightly bifid tip. Most distal pair of spines each with short, blunt, inwardly directed apophysis near base. Remaining eight erect spines each with long, slender, inwardly directed spiniform apophysis (sometimes with minutely bifid tip) near base. Ancestrula sometimes regenerated as kenozooid (Fig. 72).

**Table 9** *Puellina bifida* (d'Hondt): measurements in microns

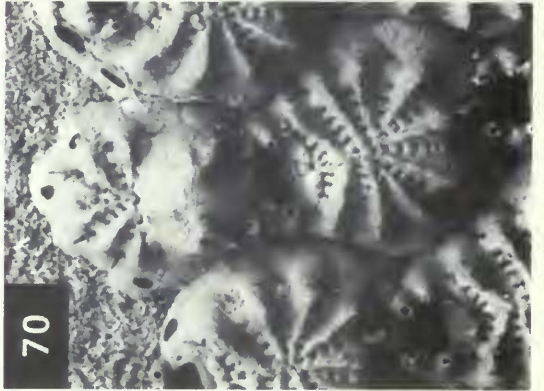
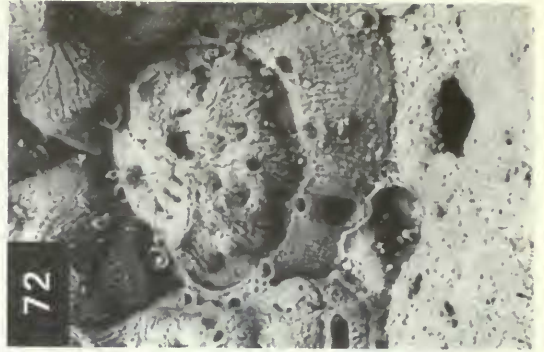
Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	43-49	45.7	4.21	9	Lf	198-246	222	7.02	12
b		39-53	47.3	7.85	10		199-252	216	7.40	9
c		52	—	—	1		204-208	206	1.54	2
d		52-59	54.7	3.89	14		187-295	233	12.0	14
e		—	—	—	0		195-271	227	9.02	16
a	lo	54-62	58.2	4.97	9	Lfg	251-332	287	9.17	12
b		59-73	65.3	7.16	8		243-318	276	10.9	8
c		71	—	—	1		252-253	253	0.314	2
d		61-73	65.9	6.15	14		227-426	327	19.1	14
e		—	—	—	0		262-407	310	15.8	15
a	loo	65-72	68.9	4.11	7	lf	149-179	162	6.30	15
b		79-81	80.0	1.99	2		142-191	173	8.26	11
c		75-78	76.5	3.12	2		169-187	178	8.04	2
d		68-79	74.0	4.96	6		158-221	188	10.7	18
e		—	—	—	0		157-200	175	7.39	14
a	Lov	148-184	167	9.28	6	Lr	—	—	—	0
b		155-173	162	5.33	4		144-148	146	2.18	2
c		—	—	—	0		136	—	—	1
d		146-198	175	12.7	5		142	—	—	1
e		154-177	164	6.15	5		—	—	—	0
a	lov	178-205	195	6.06	6	Lav	—	—	—	0
b		168-218	188	12.7	4		228-233	231	1.72	2
c		—	—	—	0		229	—	—	1
d		170-206	188	7.53	5		240	—	—	1
e		184-212	197	5.64	5		—	—	—	0

a=lectotype (LBIMM-BRY-11603); b=BMNH 1985.11.20.103a; c=BMNH 1936.12.30.331B; d=BMNH 1936.12.30.331A; e=BMNH 1911.10.1.1182B.

**Figs 62-66** *Puellina bifida* (d'Hondt): (62) ovicellate autozooid, lectotype (LBIMM-BRY-11603), off Finistère,  $\times 170$ ; (63) non-ovicellate autozooid, BMNH 1985.11.20.71a, Channel Stn 252,  $\times 240$ ; (64) abraded autozooids at edge of colony showing pore chambers, arrows indicate intact maternal autozooids (that had presumably been ovicellate), BMNH 1936.12.30.331A, no locality,  $\times 91$ ; (65) avicularium, BMNH 1985.11.20.103a, Channel Stn 261,  $\times 260$ ; (66) avicularium, regenerated non-ovicellate autozooid (on left) with abnormal orifice and maternal autozooid (on right) with ovicell not yet developed, BMNH 1936.12.30.331B, no locality,  $\times 150$ .







REMARKS. This form has apparently been overlooked since its description as a subspecies of *P. innominata*. The latitude of the type locality given by d'Hondt (1970:233) is erroneous, and he provided (pers. comm. to JDDDB, 1986) the correct position off Finistère quoted here. The type series comprised 'quelques colonies' but no holotype designation for these was published. The specimen received on loan from LBIMM, which was labelled 'holotype', is designated here as lectotype. It is not known whether this is the specimen figured by d'Hondt. The original account and figure clearly refer to the form represented by the lectotype, but are misleading in a number of respects. The supposedly bifid oral spines described by d'Hondt are in fact incomplete, broken just above the level of their inwardly directed apophyses. A minute apical avicularium on the ovicell, mentioned by d'Hondt in both the description and diagnosis and apparently shown in his figure 12a, is not to be seen in the lectotype, nor in other material examined here. The frontal shields of adjacent zooids are not separated by broad, smooth areas as apparently shown in figure 12a. Non-ovicellate zooids with 4, rather than 5, oral spines have not been observed.

*P. bifida* is extremely similar to the Badenian (Middle Miocene) fossil *P. kollmanni* (David & Pouyet, 1974) from the Vienna Basin (material of *P. kollmanni* examined by SEM: holotype and paratype, both NMV 1848/38/76; BMNH D44968 and D55589; all from Eisenstadt). The only appreciable difference between the two forms is that the avicularian palate of *P. kollmanni* is generally more elongate and slender than that of *P. bifida*, and often almost parallel sided. As mentioned above, the length of the palate in *P. bifida* is variable, and in some examples the mandible appears to pass beyond the palate as a narrow extension (Fig. 67). If it could be shown that in the latter cases the rostrum was broken short distally, the shape of the palate when complete would be inferred from the mandible to resemble that seen in *P. kollmanni*, and an argument might then be made for treating the fossil and Recent forms as conspecific.

*Puellina bifida* is also similar to the Recent Mediterranean species *P. minima* (Harmelin, 1984) of which four colonies of the type series (LBIMM, no registration number, Cassis, France) were examined by SEM. In *P. minima*, however, the ovicellate zooid has 2 oral spines, not 4. As noted by Harmelin (1984), the ovicell of *P. minima* may rest on a kenozooid (Fig. 94; ovicell category B of the present paper). This condition is also sometimes seen in *P. bifida* (Fig. 70). The material from the Canaries recorded as *C. minima* by Aristegui (1984) has 4 oral spines in the ovicellate zooid, and seems to be closer to *P. bifida* than to Harmelin's species.

*P. bifida* is known to occur off Finistère (depth 130 m); in the English Channel off Boulogne, Normandy, Brittany, Guernsey and Cornwall (at depths, where known, of 29–102 m); in the Irish Sea; and off Antrim. The presence in the Canaries of a very similar, possibly conspecific, form recorded by Aristegui (1984) as *Cribrilaria minima* suggests that *P. bifida* may also be found considerably further south than the above-mentioned localities.

### *Puellina (Cribrilaria) arrecta* n.sp.

(Figs 73–81 and Table 10)

whole or part *Cribrilaria flabellifera*: Harmelin, 1970; 94–96.

part *Cribrilaria flabellifera*: Harmelin, 1978; 186, 187 (material from Stn 72); pl. 2 figs 8, 9, 12.

*Cribrilaria flabellifera*: Hayward & Ryland, 1978; 146.

Holotype: BMNH 1985.11.20.108h (Channel Stn 314, 49°12.4'N 03°14.8'W, 73 m).

Paratypes (examined by SEM): BMNH: 1911.10.1.737A (Guernsey); 1985.11.20.76e–g (Channel Stn 253); 1985.11.20.82b (Channel Stn 256); 1985.11.20.103f (Channel Stn 261); 1985.11.20.110c (Channel Stn 314).

---

**Figs 67–72** *Puellina bifida* (d'Hondt): (67) avicularium with mandible intact, BMNH 1985.11.20.71a, Channel Stn 252, × 166; (68) kenozooid, BMNH 1936.12.30.331A, no locality, × 260; (69) avicularium regenerated as kenozooid, BMNH 1985.11.20.103a, Channel Stn 261, × 200; (70) autozooid with category B ovicell, BMNH 1936.12.30.331A, no locality, × 102; (71) ancestrula, BMNH 1985.11.20.72d, Channel Stn 252, × 230; (72) ancestrula regenerated as kenozooid, BMNH 1936.12.30.331B, no locality, × 250.

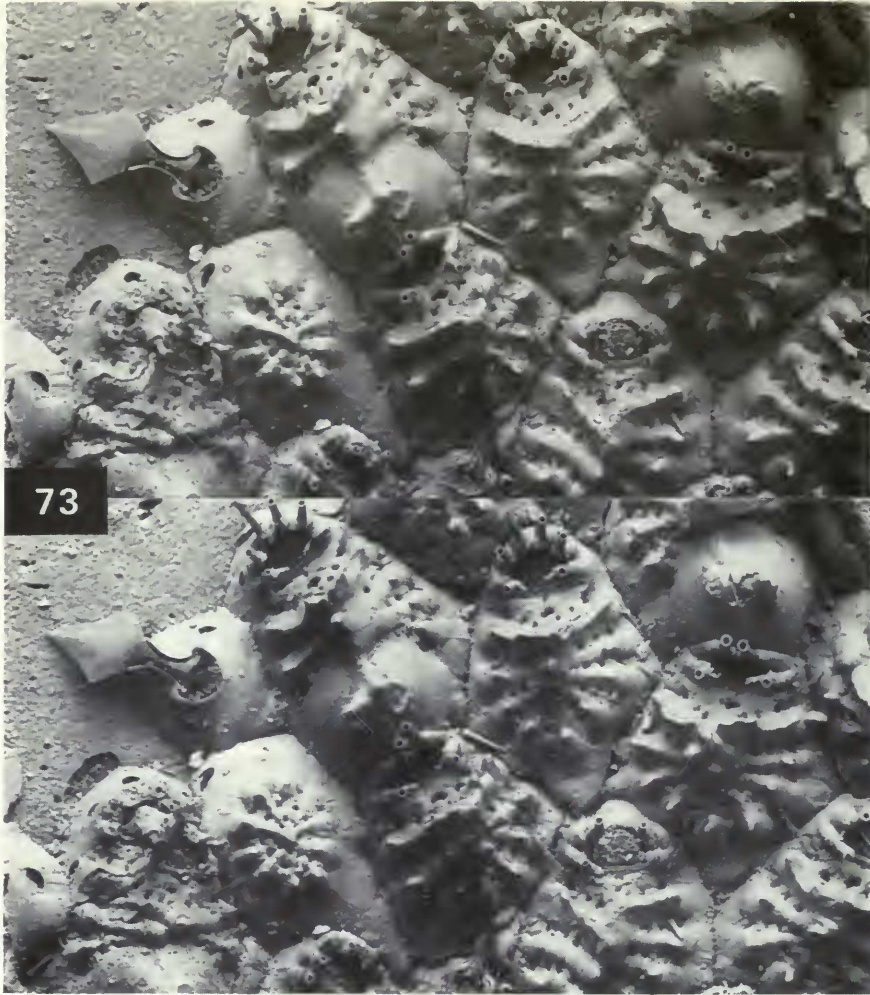


Fig. 73 *Puellina arrecta* n.sp.: stereo pair of holotype (BMNH 1985.11.20.108h), Channel Stn 314,  $\times 111$ .

OTHER MATERIAL.

BMNH: 1985.11.20.35 (northern Bay of Biscay); 1985.11.20.49 and 1985.11.20.50a (Channel Stn 247); 1985.11.20.57b (Channel Stn 249); 1985.11.20.63b and 1985.11.20.64h (Channel Stn 250); 1985.11.20.69g,h and 1985.11.20.72k (Channel Stn 252); 1985.11.20.73b, 1985.11.20.75, 1985.11.20.79 and 1985.11.20.81b,c (Channel Stn 253); 1985.11.20.84 (Channel Stn 256); 1985.11.20.85a and 1985.11.20.86 (Channel Stn 257); 1985.11.20.102c (Channel Stn 260); 1985.11.20.108i,j (Channel Stn 314).

J. G. Harmelin, personal collection: three colonies from Cassidaigne (Marseille), 350–450 m.

DESCRIPTION. Colony encrusting, unilaminar, zooids distinct; largest colonies in available material pluriserial to multiserial, with over 100 autozooids. Autozooid of variable shape in frontal

Figs 74–77 *Puellina arrecta* n.sp.: (74) whole colony, BMNH 1985.11.20.110c, Channel Stn 314,  $\times 20$ ; (75) edge of colony viewed at angle, BMNH 1985.11.20.76e, Channel Stn 253,  $\times c. 65$ ; (76) avicularium (mandible intact) and distal part of non-ovicellate autozooid, holotype (BMNH 1985.11.20.108h), Channel Stn 314,  $\times 250$ ; (77) avicularium, ovicellate and non-ovicellate autozooids, BMNH 1985.11.20.76e, Channel Stn 253,  $\times 157$ .



view, generally sub-oval (longer than broad). Lateral and proximal gymnocyst of autozooid narrow or of moderate width, but frequently with proximal or proximo-lateral extensions between neighbouring zooids.

Frontal shield (= pericyst) of autozooid heavily calcified (especially near midline), with 8 or 9 costae (rarely 7 or 10). Each costa with short, steeply ascending basal portion at periphery of frontal shield leading to less steep subsequent portion contributing to convex central region of shield. Costal ridges prominent, each with tubercle (sometimes with minute pematidium) towards periphery of shield; ridges frequently fused to form strongly raised median ridge or umbo, especially towards distal end of shield. Intercostal pores sub-rectangular or reniform, relatively uniform in size throughout shield, often with denticles adjacent to intercostal suture; usually 2 or 3 pores between successive costae. Lipped papilla pore between bases of successive costae, slightly larger than adjacent intercostal pore.

Orifice of non-ovicellate autozooid D-shaped, very clearly broader than long, proximal edge straight. Orifice of ovicellate zooid sometimes appearing distally truncate to varying extent in frontal view because of overhanging calcification of ovicell; width 1.0–1.1 times that of orifice of non-ovicellate zooid. Oral spines 6 in non-ovicellate zooid, 4 in ovicellate zooid; jointed some distance above base; most proximal spine on each side generally with inwardly directed spiniform apophysis above joint; remaining spines with inwardly directed half-circle of denticles above joint. Apertural bar sloping upwards from proximal margin of orifice to first row of intercostal pores, with median suture; often with minute pematidium on very low tubercle each side of midline. Single median sub-oral lacuna of variable shape, larger than an intercostal pore, frequently with pair of denticles on proximal margin.

Each autozooid usually with 6–8 distolateral pore chambers; uncalcified external windows of pore chambers (seen in zooids on edge of colony: Fig. 79) of moderate size but considerably larger than an intercostal pore.

Ovicell of category A (p. 4), length 0.6–0.9 times that of frontal shield; frontal surface non-punctate, with up to 3 low ridges in more or less radiating pattern; median suture occasionally discernible.

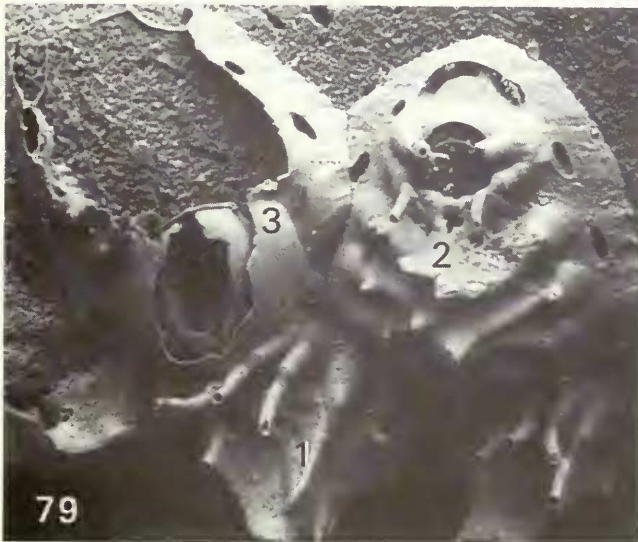
Avicularium (Fig. 76) frequent, interzooidal, total length (excluding mandible) approximately equal to that of frontal shield of autozooid. Palate flared at each end with relatively narrow middle portion; margins smooth (rarely with irregular minute crenulations). Mandible clearly longer than palate, broadening laterally beyond palate into angular-ovate or triangular blade *c.* 1.5 times as wide as frontal non-calcified area of cystid. Frontal non-calcified area sometimes occupied by cribrimorph frontal shield after regeneration as kenozooid (Fig. 78). Cystid of avicularium with 2 or 3 pore chambers. Length of proximal gymnocyst about equal to that of palate plus frontal non-calcified area.

Kenozooid (Fig. 73) fairly frequent, up to size of autozooid, with cribrimorph frontal shield of costae in radiating pattern.

Ancestrula (Fig. 80) tatiform, with median proximal spine overarching frontal surface plus 5 pairs of erect spines around edge of gymnocyst (i.e. total of 11 spines). Erect spines jointed, with at least 2 segments above base. Median proximal spine with broad or bifid tip. Most distal pair of spines each with short, inwardly directed apophysis near base. Remaining eight erect spines each with inwardly directed spiniform apophysis near base. Ancestrula sometimes regenerated as kenozooid (Fig. 81).

ETYMOLOGY. *L. arrectus*—upright, steep; referring to the form of the frontal shield in this species.

REMARKS. This species is most closely comparable to *P. flabellifera* (Kirkpatrick, 1888) with which it has been confused and which is redescribed below. The autozooids have more extensive exposed gymnocyst in *Puellina arrecta* n.sp. than in *P. flabellifera*. There are considerable differences in the form of the frontal shield between the two species. The frontal shield of *P. arrecta* is markedly convex whereas that of *P. flabellifera* is almost flat. There are fewer costae in *P. arrecta*. The costae all bear a ridge and/or tubercle in the newly described species, whereas only the most distal pair have distinct ornamentation (ridges) in *P. flabellifera*. The median umbo of *P. flabellifera* (when



**Figs 78–81** *Puellina arrecta* n.sp.: (78) kenozooid and avicularium regenerated as kenozooid, BMNH 1985.11.20.110c, Channel Stn 314,  $\times 230$ ; (79) maternal autozooids (numbered 1 and 2) and developing autozooid (numbered 3) with incomplete category A ovicell for zooid 1, holotype (BMNH 1985.11.20.108h), Channel Stn 314,  $\times 155$ ; (80) ancestrula and first autozooid (developed to right of midline of ancestrula because of foreign body distal to ancestrula), BMNH 1985.11.20.76g, Channel Stn 253,  $\times 200$ ; (81) ancestrula regenerated as kenozooid, holotype,  $\times 250$ .

**Table 10** *Puellina arrecta* n.sp.: measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	36-45	38.8	11.0	5	Lf	163-209	187	8.85	10
b		43-47	44.7	2.90	7		187-204	193	3.58	8
c		41	—	—	1		179-193	184	2.90	8
d		40-45	42.6	4.48	11		154-210	185	7.72	18
a	lo	57-65	61.0	5.30	5	Lfg	203-291	253	14.2	9
b		65-75	70.0	6.79	5		244-312	276	8.69	8
c		58	—	—	1		213-291	248	11.0	6
d		59-71	65.3	6.39	7		233-325	272	11.1	16
a	loo	63-65	64.0	2.49	2	lf	148-178	163	6.60	11
b		64-70	66.7	4.96	3		144-181	159	8.21	10
c		—	—	—	0		135-151	146	4.23	7
d		69-74	71.0	2.77	5		135-178	155	7.21	16
a	Lov	143-163	151	6.22	4	Lr	109-114	112	3.57	2
b		115-146	133	10.2	5		113-132	122	6.86	5
c		125-150	138	8.48	4		—	—	—	0
d		128-157	147	7.08	6		91-127	115	13.0	6
a	lov	155-203	181	12.5	4	Lav	208-220	214	4.47	2
b		163-193	182	6.59	5		201-262	224	11.2	5
c		170-184	177	4.31	3		—	—	—	0
d		165-180	171	4.43	6		198-296	253	16.2	5

a = holotype (BMNH 1985.11.20.108h); b = BMNH 1985.11.20.76e; c = BMNH 1911.10.1.737A; d = BMNH 1985.11.20.110c.

present) is restricted to the region of the first pair of costae, but that of *P. arrecta* generally extends proximally as a median ridge. The sub-oral lacuna is relatively smaller in *P. arrecta*, and the orifice wider but shorter. The margins of the avicularian palate are generally smooth in *P. arrecta* rather than crenulate as in *P. flabellifera*. The mandible of the avicularium is relatively small in *P. arrecta*, and broadens beyond the palate to less than twice the width of the frontal non-calcified area of the avicularian cystid, as opposed to *c.* three times the width in *P. flabellifera*.

BMNH 1985.11.20.35 is part of the material recorded as *Cribrilaria flabellifera* by Hayward & Ryland (1978). Material from the Marseille region at a depth of 350-450 m recorded as *C. flabellifera* by Harmelin (1970) was examined on loan, and is also referred to *P. arrecta* n.sp. Harmelin's material from 105-110 m in the same region was not examined.

*P. arrecta* is known from the English Channel off Brittany (depths 64-106 m) and Guernsey, from the northern Bay of Biscay at a depth of 180-182 m, and from the Mediterranean near Marseille (depth 350-450 m).

***Puellina (Cribrilaria) flabellifera* (Kirkpatrick, 1888)**

(Figs 92, 93 and Table 11)

*Cribrilaria radiata* var. *flabellifera* Kirkpatrick, 1888; 75, pl. 10 fig. 4.

Lectotype (selected here): BMNH 1888.1.25.10A (Mauritius).

DESCRIPTION OF LECTOTYPE. Fragment of unilaminar colony, zooids distinct, *c.* 90 autozooids and *c.* 50 avicularia. Autozooid of variable shape in frontal view, generally sub-oval (longer than



broad). Exposed lateral gymnocyst of autozoid narrow or absent (except at edge of colony); proximal gymnocyst narrow, but occasionally with short proximal extension(s) between neighbouring zooids.

Frontal shield (=pericyst) of autozoid moderately calcified, without differential median thickening apart from distal umbo (see below), generally with 14 or 15 costae (occasionally 16). Each costa with short, steeply ascending basal portion at periphery of frontal shield leading to nearly horizontal subsequent portion, of relatively constant width, contributing to almost flat central region of shield. Most distal pair of costae forming shallow V in frontal view, ridges prominent and frequently forming truncate median umbo. Remaining costae low, lacking distinct ornamentation. Intercostal pores sub-rectangular or reniform, relatively uniform in size throughout shield, frequently with denticles adjacent to intercostal suture; usually 4 or 5 pores between successive costae, but fewer between short proximal costae. Lipped papilla pore between bases of successive costae.

Orifice of non-ovicellate autozoid D-shaped, slightly broader than long, proximal edge straight. Orifice of ovicellate zoid generally appearing distally truncate in frontal view because of overhanging calcification of ovicell; width 1.1–1.2 times that of orifice of non-ovicellate zoid. Oral spines 6 in non-ovicellate zoid, 4 in ovicellate zoid; jointed some distance above base, apparently without apophyses (but undamaged spines not observed). Apertural bar sloping slightly upwards from proximal margin of orifice towards first pair of costae; without tubercles; sometimes with minute pelmatidium each side of median suture. (Pelmatidia not observed elsewhere on shield.) Single median sub-oral lacuna very large (considerably larger than an intercostal pore), of variable shape, frequently with denticles on lateral and proximal margins.

Characters of pore chambers not discernible.

Ovicell of category A (p. 4), length generally 0.6–0.7 times that of frontal shield of autozoid; frontal surface non-punctate, frequently with up to 4 ridges in more or less radiating pattern (or occasionally with short median ridge), with median suture.

Avicularium frequent, interzooidal, total length excluding mandible approximately equal to that of frontal shield of autozoid. Palate flared at each end, more so distally, with relatively narrow middle portion; margins crenulate. Mandible clearly longer than palate, broadening abruptly beyond palate to *c.* 3 times width of frontal non-calcified area; further details of shape not discernible because of damage. Length of proximal gymnocyst of avicularium about equal to that of palate plus frontal non-calcified area. Cystid with pore chamber windows, 3 in only example counted.

Kenozooid infrequent, smaller than an autozoid, with cribrimorph frontal shield of costae in radiating pattern.

Colony origin, including ancestrula, missing.

REMARKS. Kirkpatrick (1888: pl. 10 fig. 4) illustrated the undamaged avicularian mandible broadening rapidly beyond the palate into a sub-triangular blade. Neither Kirkpatrick's account nor the relevant BMNH accessions book indicates how many colonies were originally referred to

**Table 11** *Puellina flabellifera* (Kirkpatrick): measurements on lectotype (BMNH 1888.1.25.10A) in microns

	Range	Mean	C.V.	n		Range	Mean	C.V.	n
Lo	45–53	48.6	6.32	13	Lf	184–271	213	12.6	10
lo	51–65	58.2	7.08	10	Lfg	237–340	283	12.7	11
loo	64–70	67.3	4.92	3	lf	152–208	184	8.77	15
Lov	122–167	149	12.4	5	Lr	119–156	138	11.2	15
lov	145–171	157	7.44	5	Lav	240–316	269	8.36	15

*Cribrilina radiata* var. *flabellifera*. Two specimens from Mauritius, stored separately but both registered as BMNH 1888.1.25.10, are the only available material referable to the original description. The specimen on a microslide, clearly the form described by Kirkpatrick and labelled 'Type', is presumably that examined by Harmelin (1978); it is here selected as lectotype (now BMNH 1888.1.25.10A). It is not possible to identify the lectotype positively as the specimen figured by Kirkpatrick. However the second, boxed, specimen (now 1888.1.25.10B) apparently grew on a different substrate from the lectotype, and is not the same species but a form with a slender elongate-triangular avicularian mandible, probably *P. africana* (Hayward & Cook, 1983).

Kirkpatrick's variety was elevated to species rank by Harmelin (1970). In addition to the original description and another record from the Indian Ocean (Thornely, 1912), the name *flabellifera* has been applied to material from the Indonesian region (Harmer, 1926; Canu & Bassler, 1929a; Winston, 1986), the central Pacific (Harmelin, 1978), the eastern Pacific (Soule, 1959), the western Caribbean (Banta & Carson, 1978; Winston, 1984), the Mediterranean (Harmelin, 1970) and the

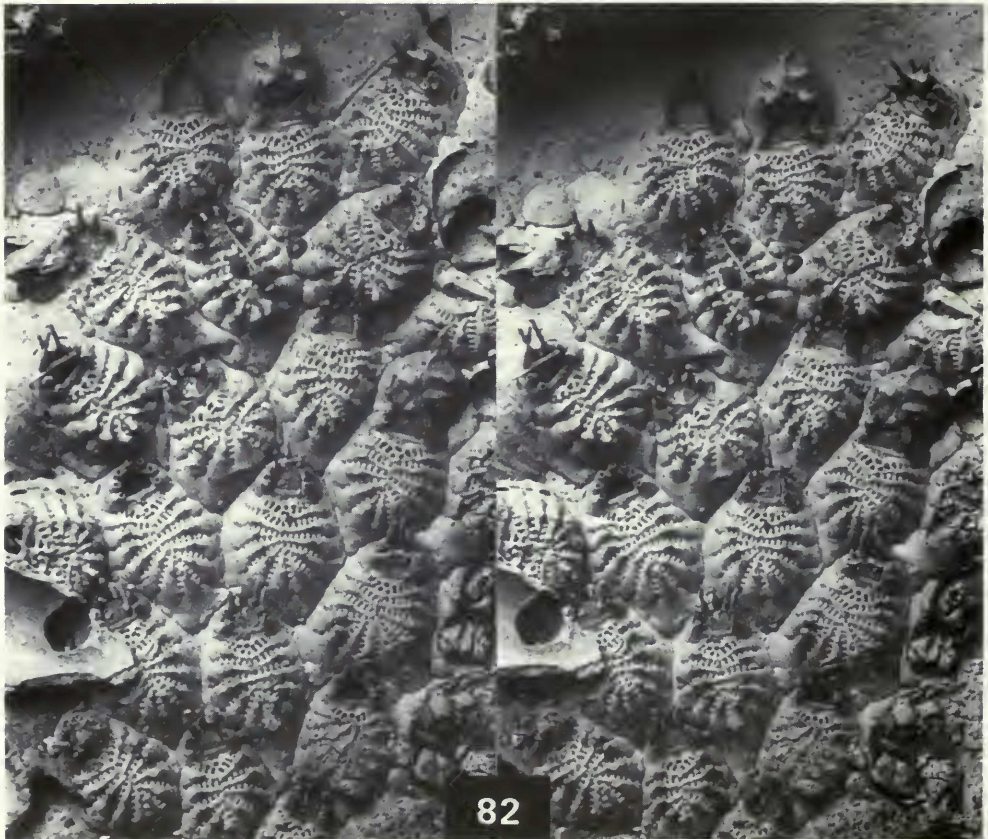


Fig. 82 *Puellina corbula* n.sp.: stereo pair of holotype (BMNH 1985.11.20.80), Channel Stn 253,  $\times 62$ .

Figs 83–87 *Puellina corbula* n.sp.: (83) ovicellate and non-ovicellate autozooids at edge of colony, holotype (BMNH 1985.11.20.80), Channel Stn 253,  $\times 133$ ; (84) edge of colony viewed at angle, holotype,  $\times 72$ ; (85) avicularium recumbent on neighbouring autozooid, holotype,  $\times 350$ ; (86) semi-erect avicularia at edge of colony, with ovicellate and non-ovicellate autozooids, BMNH 1985.11.20.100b, Channel Stn 260,  $\times 158$ ; (87) kenozooid, ovicellate and non-ovicellate autozooids at edge of colony, BMNH 1911.10.1.735B, Belfast,  $\times 112$ .



eastern Atlantic (Harmelin, 1978; Hayward & Ryland, 1978; d'Hondt, 1979; Aristegui, 1983; 1984). It seems probable that a species group, rather than a single species, is involved. At least part of Harmelin's (1970) Mediterranean material, part of the NE. Atlantic material recorded by the same author (1978), and the record by Hayward & Ryland (1978) from the northern Bay of Biscay, are referred to *P. arrecta* n.sp. above.

*Puellina (Glabrilaria) corbula* n.sp.

(Figs 82–91 and Table 12)

part *Cribrilaria pedunculata*: Harmelin 1978; 188, 189 (material from Stn 72); pl. 1 fig. 5; not pl. 1 fig. 6.

Holotype: BMNH 1985.11.20.80 (Channel Stn 253, 48°52'2"N 03°54'0"W, 79 m).

Paratypes (examined by SEM): BMNH: 1911.10.1.735B (Belfast); 1985.11.20.72c (Channel Stn 252); 1985.11.20.100a,b,c (Channel Stn 260); 1985.11.20.108a and 1985.11.20.109a (Channel Stn 314).

OTHER MATERIAL.

BMNH: 1911.10.1.731 (British); 1985.11.20.52a (Channel Stn 248); 1985.11.20.59a (Channel Stn 249); 1985.11.20.69a and 1985.11.20.72a,b (Channel Stn 252); 1985.11.20.74a,b (Channel Stn 253); 1985.11.20.99 and 1985.11.20.101 (Channel Stn 260).

DESCRIPTION. Colony encrusting, unilaminar, zooids distinct; largest colonies in available material pluriserial to multiserial, with over 200 autozooids. Autozoid of variable shape in frontal view, generally round or sub-oval (longer than broad). Lateral and proximal gymnocyst of autozoid narrow to broad, but generally of moderate width and frequently with proximal and proximo-lateral extensions between neighbouring zooids.

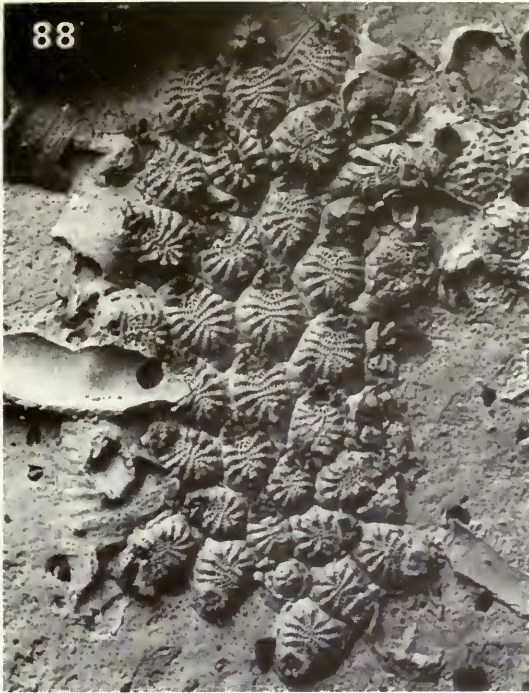
Frontal shield (= pericyst) of autozoid lightly to moderately calcified, without umbo or any other median thickening, with 9–14 costae (usually 10–12). Each costa with broad, steeply ascending basal portion at periphery of frontal shield leading to narrower, tapering, nearly horizontal subsequent portion contributing to almost flat central region of shield, and with tubercle or short ridge (frequently bearing pematidium) near base. Intercostal pores sub-rectangular or reniform, generally slightly larger in first intercostal row (i.e. just proximal to orifice) than in remainder of shield, frequently with denticles adjacent to intercostal suture; intercostal pores present along entire length of costae (i.e. not restricted to nearly horizontal region of shield as in many other species: Fig. 83); usually 6–8 pores between successive costae, but occasionally fewer between short proximal costae. Papilla pore between bases of successive costae inconspicuous, about size of adjacent intercostal pore.

Orifice of non-ovicellate autozoid D-shaped, slightly broader than long, proximal edge straight. Orifice of ovicellate zooid occasionally appearing slightly truncate in frontal view because of overhanging calcification of ovicell; width 1.2–1.3 times that of orifice of non-ovicellate zooid. Operculum sometimes with central tubercle (Fig. 89, partially obscured). Oral spines 7 in non-ovicellate zooid, 4 in ovicellate zooid; jointed some distance above base with 2 (possibly more) subsequent segments, without inwardly directed apophyses. Distal portion of apertural bar frequently sloping downwards from proximal margin of orifice towards sub-oral lacunae; proximal portion ascending or flat; apertural bar with pematidium each side of midline, without tubercles. One or 2 (rarely 3) median sub-oral lacunae between proximal margin of orifice and first row of intercostal pores, of variable shape, about same size as a large intercostal pore, occasionally divided in two by median denticle.

Each autozoid with *c.* 7 distolateral pore chambers; uncalcified external windows of pore chambers (seen in zooids on edge of colony: Fig. 84) of moderate size but considerably larger than an intercostal pore.

Ovicell of category C (p. 4), length 0.7–0.8 times that of frontal shield; frontal surface non-punctate, frequently with 4–6 low ridges in more or less radiating pattern; median suture not observed.

Avicularium (Figs 85, 86) minute, infrequent to fairly frequent; palate elongate-triangular, inclined at steep angle to substrate (except one example in holotype, with rostrum recumbent on



**Figs 88–91** *Puellina corbula* n.sp.: (88) whole colony, holotype (BMNH 1985.11.20.80), Channel Stn 253,  $\times 36$ ; (89) non-ovicellate autozooid, holotype,  $\times 270$ ; (90) ancestrula and first autozooid, BMNH 1985.11.20.72c, Channel Stn 252,  $\times 191$ ; (91) ancestrula regenerated as kenozooid, holotype,  $\times 230$ .

neighbouring autozoid; Fig. 85); rostrum curved at extreme tip to form very small beak-like projection. Mandible elongate-triangular, slightly shorter than palate. Cystid of avicularium forming short, sub-conical, semi-erect support for rostrum; with 1 or 2 pore chamber windows near base.

Kenozooid (Fig. 87) infrequent, with cribrimorph frontal shield of costae in radiating pattern.

Ancestrula (Fig. 90) tatiform, with 5 pairs of spines plus unpaired proximal and distal median spines (i.e. total of 12 spines) around edge of gymnocyst. Median proximal spine overarched frontal surface, with tapering, pointed tip; remaining spines erect, without inwardly directed (or other) apophyses. Details of jointing of spines not clearly seen, but at least some erect spines jointed at base and with at least 2 subsequent segments. Ancestrula sometimes regenerated as kenozooid (Fig. 91).

**Table 12** *Puellina corbula* n.sp.: measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	51-62	56.6	6.21	14	Lf	198-263	225	7.72	17
b		57-69	62.4	4.23	8		214-257	235	5.92	13
c		58-67	62.6	5.01	10		229-270	245	4.82	17
d		54-61	57.4	4.50	8		201-243	222	5.45	20
a	lo	57-68	62.7	4.69	14	Lfg	261-450	311	15.2	16
b		68-73	70.3	1.80	8		264-349	304	9.10	13
c		66-80	70.5	6.50	8		262-373	324	11.0	16
d		57-66	60.7	5.50	15		245-341	278	8.92	20
a	loo	69-78	73.5	9.74	2	lf	172-225	193	6.99	17
b		78-89	83.8	4.78	4		187-243	217	7.95	12
c		83-88	86.0	3.34	3		195-243	226	5.75	17
d		71-80	76.8	5.46	4		179-233	204	7.38	19
a	Lov	152-153	153	0.522	2	Lr	114	—	—	1
b		145-159	152	4.99	3		—	—	—	0
c		151-172	160	4.50	6		—	—	—	0
d		174-182	178	2.31	4		—	—	—	0
a	lov	186-192	189	2.53	2	Lav	149	—	—	1
b		192-199	196	1.95	3		—	—	—	0
c		182-198	194	3.32	6		—	—	—	0
d		196-222	211	5.50	4		—	—	—	0

a = holotype (BMNH 1985.11.20.80); b = 1985.11.20.100b; c = 1985.11.20.100c; d = BMNH 1911.10.1.735B.

**ETYMOLOGY.** *L. corbula*—a little basket; referring to the form of the frontal shield in this species.

**REMARKS.** *Puellina corbula* n.sp. is most closely comparable with *P. africana* (Hayward & Cook, 1983), of which two paratype colonies from the E. coast of South Africa (BMNH 1983.11.5.75) have been examined by SEM. The steeply ascending basal portion of each costa is relatively much shorter in *P. africana* than in *P. corbula* so that the frontal shield is considerably less raised overall. Unlike *P. corbula*, the costae of *P. africana* are without distinct ornamentation (the small tubercles noted in the original description not being apparent in the material examined). The avicularian rostrum is much more elongate in *P. africana*, and avicularia commonly occur closely applied to the sides of ovicells, a position they rarely occupy in *P. corbula*.

*P. corbula* is also similar to the Mediterranean species *P. pedunculata* Gautier, 1956, with which it has been confused (and which is redescribed below). In Gautier's species the frontal shield is more evenly convex, and the costae lack any trace of the tubercles or short ridges commonly seen near their base in *P. corbula*. Non-ovicellate autozooids of *P. corbula* have 7 oral spines, but there are only 6 in *P. pedunculata*. The avicularium of *P. corbula* has a relatively broad base (with 1 or 2 pore chamber windows) generally seen to rest on the substrate, and tapers from the base towards the rostrum, whereas that of *P. pedunculata* is fully erect and broadens slightly from a narrow base (without pore chamber windows) approximately equal in area to the uncalcified external window of the pore chamber from which it was budded. Unlike *P. pedunculata*, no area of kenozooidal costate frontal shield is seen distal to the ovicell in *P. corbula* (category C rather than category B ovicell as defined on p. 4). The ovicell of *P. corbula* is larger than that of *P. pedunculata*, both in absolute terms and relative to the respective autozooids, and generally has several ridges in a more or less radiating pattern rather than a single longitudinal ridge.

*P. corbula* is known from the English Channel off Brittany at depths of 73–106 m, and also from a single specimen (BMNH 1911.10.1.735B) labelled simply 'Belfast'. Specimens very similar to *P. corbula* n.sp. also occur in the Mediterranean near Marseille (J. G. Harmelin, pers. comm. to JDDB, 1986). In Harmelin's material tubercles or short ridges near the base of the costae are poorly developed or absent, and the frontal shield has a more evenly arched appearance than is usual in the material described here. However, the avicularium and ovicell are typical of *P. corbula*, and it seems probable that the Atlantic and Mediterranean forms are conspecific. This record allows the possibility that *P. corbula* is merely a geographical variant of *P. pedunculata* to be discounted, since the type locality of Gautier's species is near Marseille.

### *Puellina (Glabilaria) pedunculata* Gautier, 1956

(Figs 95–97 and Table 13)

*Puellina pedunculata* Gautier, 1956; 203, fig. 20.

*Colletosia pedunculata*: Prenant & Bobin, 1966; 596, 597, fig. 207III.

not *Colletosia pedunculata*: Harmelin, 1968; 1199, fig. 3(5).

*Cribrilaria pedunculata*: Harmelin, 1970; 93, 94, fig. 1g,h, pl. 2 fig. 6.

not *Cribrilaria pedunculata*: Harmelin, 1978; 188, 189 (material from Stn 72), pl. 1 fig. 5 (= *Puellina corbula* n.sp.).

#### MATERIAL EXAMINED BY SEM.

Type series: LBIMM-BRY-10384 (Marseille, two colonies on separate substrates; lectotype selected below).

BMNH: 1970.6.1.13 (Marseille).

#### OTHER MATERIAL.

BMNH: 1975.1.12.185 (Chios).

**DESCRIPTION.** Colony encrusting, unilaminar, zooids distinct; largest colony in available material with *c.* 55 autozooids. Autozooid of variable shape in frontal view, generally round or sub-oval (longer than broad). Lateral and proximal gymnocyst of autozooid narrow or of moderate width, frequently with proximal and proximo-lateral extensions between neighbouring zooids.

Frontal shield (= pericyst) lightly to moderately calcified, with little or no differential median thickening and no umbo, with 10–15 costae (usually 11–13). Each costa with short moderately to steeply ascending basal portion leading to tapering or parallel-sided nearly horizontal subsequent portion contributing to slightly convex central region of shield. Costae lacking distinct ornamentation; pematidia not observed. Intercostal pores sub-rectangular, relatively uniform in size throughout shield, sometimes with indistinct denticles adjacent to intercostal suture; 3–7 pores between successive costae. Lipped papilla pore between bases of successive costae, larger than adjacent intercostal pore.

Orifice of non-ovicellate autozooid D-shaped, clearly broader than long, proximal edge straight. Orifice of ovicellate zooid sometimes appearing distally truncate in frontal view because of overhanging calcification of ovicell (BMNH 1970.6.1.13); width *c.* 1.1 times that of orifice of non-ovicellate zooid. Oral spines 6 in non-ovicellate zooid, 4 in ovicellate zooid, jointed some distance





above base; further details of spine morphology not seen. Distal portion of apertural bar frequently sloping steeply downwards from proximal margin of orifice; proximal portion of apertural bar sloping slightly upwards to first pair of costae; without pematidia or tubercles, but median suture often discernible. Usually 2 median sub-oral lacunae, each about size of an intercostal pore, sometimes with indistinct denticles on proximal margin.

Each autozoid with *c.* 10 distolateral pore chambers; uncalcified external windows of pore chambers (seen in zooids on edge of colony) of moderate size but considerably larger than an intercostal pore.

Ovicell of category B (p. 4), with relatively small area of kenozooidal frontal shield (Fig. 95), length 0.5–0.7 times that of frontal shield of autozoid; frontal surface non-punctate, with low median ridge along entire length, frequently with central umbo.

Avicularium (Figs 95, 97) minute, frequent, often budded from kenozooid. Palate elongate-triangular, inclined at steep angle to substrate. Mandible elongate-triangular, slightly shorter than palate. Cystid erect, arising from very narrow base, an elongate, inverted cone, without pore chamber windows.

Kenozooid (Fig. 96) frequent, of variable size and shape but always smaller than autozoid, with strongly convex cribrimorph frontal shield of costae in radiating pattern. Each ovicell invariably associated with a kenozooid, as noted above.

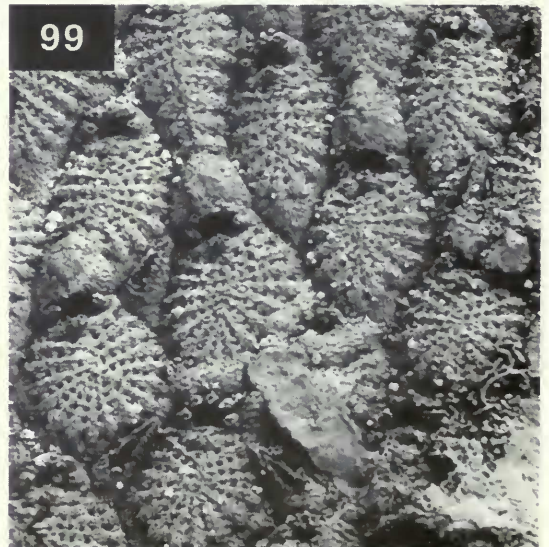
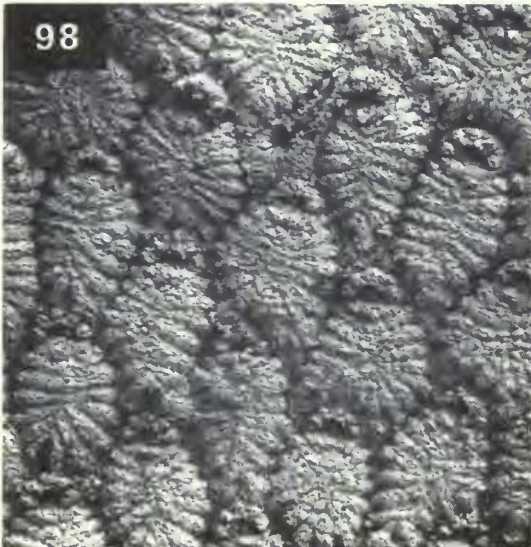
Ancestrula obscured in available material.

**Table 13** *Puellina pedunculata* Gautier: measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	47–50	48.8	2.74	4	Lf	194–233	213	5.51	14
b		40–55	45.2	13.3	5		167–203	187	6.47	12
c		43–46	44.5	5.37	2		199–241	215	5.29	13
a	lo	66–70	67.5	2.73	4	Lfg	230–323	271	9.07	14
b		60–64	61.6	2.86	5		193–297	243	12.4	13
c		63–71	67.0	4.29	6		235–312	266	8.56	10
a	loo	67–80	72.1	5.35	9	lf	168–256	204	10.4	13
b		64–69	66.7	4.09	3		150–187	164	8.55	11
c		69–79	73.7	7.40	3		160–205	175	7.98	13
a	Lov	103–115	109	3.96	9	Lr	66–85	73.0	11.2	6
b		105–118	108	5.46	5		67–77	70.1	5.00	7
c		120–152	132	10.1	6		66–72	68.6	3.99	5
a	lov	115–153	140	7.74	9	Lav	156–158	157	1.01	2
b		126–135	131	2.66	6		—	—	—	0
c		148–160	155	4.48	3		—	—	—	0

a = lectotype (LBIMM-BRY-10384); b = paralectotype (LBIMM-BRY-10384); c = BMNH 1970.6.1.13.

**Figs 92–95** (92) *Puellina flabellifera* (Kirkpatrick): part of colony with avicularia, ovicellate and non-ovicellate autozooids, lectotype (BMNH 1888.1.25.10A), Mauritius,  $\times 74$ ; (93) *P. flabellifera* (Kirkpatrick): avicularia (mandibles damaged) and non-ovicellate autozooids, lectotype,  $\times 145$ ; (94) *Puellina minima* (Harmelin): autozoid with category B ovicell and non-ovicellate autozoid at edge of colony, type series (LBIMM), Cassis, France,  $\times 118$ ; (95) *Puellina pedunculata* Gautier: category B ovicell with distal avicularium, BMNH 1970.6.1.13, Marseille,  $\times 280$ .



**Figs 96–99** (96) *Puellina pedunculata* Gautier: part of colony with avicularia, kenozooids, ovicellate and non-ovicellate autozooids, lectotype (LBIMM–BRY–10384), Marseille,  $\times 87$ ; (97) *Puellina pedunculata* Gautier: distal part of autozooid with category B ovicell (kenozooidal frontal shield largely obscured) and avicularia, lectotype,  $\times 220$ ; (98) *Puellina scripta* (Reuss): avicularium (centre, near top) and non-ovicellate autozooids, holotype (NMV 1848/38/75), Badenian, Eisenstadt,  $\times 54$ ; (99) *Puellina venusta* Canu & Bassler: avicularia, ovicellate and non-ovicellate autozooids, BMNH D55588, Badenian, Hartl-lucke, Eisenstadt,  $\times 56$ .

REMARKS. Three craniid brachiopod valves were sent on loan from LBIMM as substrates of the type series of *P. pedunculata*. One of these was apparently unencrusted, but the other two each bore a colony of *P. pedunculata*. The colony illustrated in Figures 96 and 97 is selected here as lectotype. Neither of the available specimens could be identified as that illustrated by Gautier (1956).

The constant association of the ovicell with an underlying kenozooid in this species does not seem to have been remarked on before. However, a similar arrangement was noted by Harmelin (1978) in his description of the closely related species *Cribrilaria cristata*. Gautier (1956, 1962) and Prenant & Bobin (1966) indicated pores on the ovicell of *P. pedunculata*. These are not in fact present.

## Discussion

The use of SEM has been of considerable assistance in the initial discrimination of morphologically similar species of *Puellina*. However, the routine identification of the great majority of colonies of the species dealt with here can be undertaken with a suitable light microscope. Table 14 gives characters by which this may be achieved. Determination of the ovicell category (p. 4) is perhaps the best starting point for an identification.

The present account significantly increases the diversity of *Puellina* known from the British Isles. In the most recent systematic treatment of the British cribrimorph fauna, Hayward & Ryland (1979) recognised four species of *Puellina* and *Cribrilaria*. Of these, *P. setosa* was included only tentatively and is not in fact of proven British occurrence (see above). It is now necessary to add *P. modica* n.sp., *P. praecox* n.sp., *P. bifida*, *P. arrecta* n.sp. and *P. corbula* n.sp. to the list, although *P. arrecta* qualifies only through a record from Guernsey; a sixth species, *P. directa* n.sp., occurs in the English Channel off Normandy and Brittany but has not so far been recorded from the Channel Isles. *P. arrecta* and *P. corbula* were recorded from the English Channel by Harmelin (1978) as *Cribrilaria flabellifera* and *C. pedunculata* respectively. The record of *C. flabellifera* from the English Channel by d'Hondt (1979) may similarly refer to *P. arrecta*.

Available material of Recent British *Puellina* has a marked southerly and westerly bias, with the North Sea unrepresented. This is probably not entirely a reflection of collection bias. Shell substrates from the western English Channel may have a remarkably high diversity of encrustation, with 6 (BMNH 1985.11.20.69) or 7 (BMNH 1985.11.20.72) species of *Puellina* on a single small shell. All nine of the species reported here from British and adjacent waters may be found in the western English Channel, although *P. gattyae* was not recorded on shell material offshore in this area.

Four species found in British and adjacent waters also occur in the Mediterranean: *P. gattyae*, *P. venusta*, *P. arrecta* n.sp. and *P. corbula* n.sp. In addition, *P. innominata* is evidently very closely related to *Cribrilaria innominata* form B in the sense of Harmelin (1970) from the Mediterranean, and *P. bifida* bears considerable resemblance to the Mediterranean species *P. minima* (Harmelin, 1984). *P. modica* n.sp., *P. praecox* n.sp. and *P. directa* n.sp. are not known from the Mediterranean. *P. setosa*, *P. radiata* (Moll, 1803), *P. cassidainsis* (Harmelin, 1984), *P. pedunculata* Gautier, 1956 and *P. pedunculata* in the sense of Harmelin (1968) (which is considered distinct from Gautier's species) occur in the Mediterranean but have not been found in the vicinity of the British Isles.

Harmelin (1984) treated *Puellina* and *Cribrilaria* as separate genera, and laid particular stress on the form of the ovicell in differentiating between them. Conversely, Gordon (1984) treated *Cribrilaria* as a subgenus of *Puellina*, citing the presence of setiform papillae, a sub-oral lacuna and a pinnate pattern of costae as similarities which outweighed any differences between the two groups. Whilst Gordon's argument is not regarded as conclusive, his arrangement is adopted here, at least in part because difficulties have been encountered with the application of the criterion of ovicell type. Two of the newly described species, *P. praecox* and *P. directa*, have ovicells at variance with their other characters and hence fall between *Puellina* and *Cribrilaria*. Thus *P. praecox* has ovicells of category C (p. 4), yet in many other respects resembles a species of *Cribrilaria*. *P. directa* has ovicells of category A but otherwise, at least superficially, resembles a species of *Puellina*. The

**Table 14** Key characters for the identification of *Puellina* from British and adjacent waters. (\*Although *P. setosa* is included in this table, its occurrence in the area is unproven.)

	<i>P. gattya</i>	<i>P. setosa</i> *	<i>P. modica</i>	<i>P. directa</i>	<i>P. praecox</i>	<i>P. venusta</i>	<i>P. immominata</i>	<i>P. bifida</i>	<i>P. arrecta</i>	<i>P. corbula</i>
Ovicell type (see p. 4)	C	C	C	A	C	A	A	A (or B)	A	C
Median umbo of costate frontal shield	Variable, none to very large	None or very small	None	None	None	Moderate sub-oral mucro	Large	None	Very large	None
Relief of costate frontal shield	Slightly to strongly convex	Almost flat to slightly convex	Moderately convex	Strongly convex	Edges steep; centre slightly convex	Edges steep; centre slightly convex	Edges steep; centre slightly convex	Edges steep; centre slightly convex	Strongly convex	Edges steep; centre almost flat
Costae: usual number (range)	7 or 8 (5-9)	9 or 10 (7-12)	5 (4-6)	7 or 8 (7-10)	8 to 10 (8-10)	15 to 18 (12-23)	11 or 12 (9-14)	7 to 9 (6-11)	8 or 9 (7-10)	10 to 12 (9-14)
Ornamentation of costa	None	None	Strong ridge, higher towards edge of shield	Strong ridge, often higher towards centre of shield	Ridge, higher towards edge of shield	None	Ridge (variable) and/or tubercle near edge of shield	Ridge, higher towards edge of shield	Ridge and/or tubercle near edge of shield	Tubercle or short ridge near edge of shield
Proximal gymnocyst	Broad	Broad	Broad	Broad	Narrow	None or very narrow	Narrow or moderate	Narrow or moderate	Narrow or moderate	Variable, generally moderate
Oral spines (non-ovicellate)	5	5	5	5	5	5	5	5	6	7
Oral spines (ovicellate)	2	2	2	2	4	4	4	4	4	4
External windows of pore chambers	Small	Small	Small	Variable, generally small	Small	Large	Large	Large	Moderate	Moderate
Avicularium	None	None	None	None	None	Frequent	Infrequent to fairly frequent	Infrequent	Frequent	Infrequent to fairly frequent
Additional comments	Single, round intercostal pore (plus 1 papilla pore) between successive costae	First pair of costae slightly more prominent than rest	Prominent costae converge to single point	Distal pairs of costae arranged in parallel lines	Lightly calcified colonies of very few zooids	Most distal intercostal pores largest	Sub-oral lacuna large	Costal ridges often stepped in height	Avicularium with distinctive palate and mandible	Avicularium minute, semi-erect. No setiform papillae

occurrence in *P. bifida* and *P. minima* of ovicells of categories A and B in the same colony, and the evident resemblance of *P. praecox* to *P. bifida*, suggests that the conversion of one ovicell type into another may not be a particularly difficult evolutionary step. It is possible to envisage the transformation of category A into category B by the development of a distal kenozooid rather than an autozooid. Reduction in the size of the kenozooidal costate frontal shield until none was retained would then yield category C (in which the ovicell would nevertheless be regarded as kenozooidal in nature). Such a transformation of category A through B to C, which is considerably easier to envisage than the reverse pathway, may have occurred more than once within the *Puellina* clade. If so, the category C pattern of ovicell development would be a homoplasious character within the genus.

In most species with ovicells of category A, ontogenetically complete maternal autozooids are commonly seen on the edge of the colony before the budding of the distal autozooid with proximal ovicell commences. In this condition, maternal autozooids may be recognised by their reduced number of oral spines (compared with non-maternal autozooids) which are closely spaced near the proximo-lateral corners of the orifice, and by the large U-shaped distal pore (? pore chamber window) in place of the smaller sub-oval pore chamber window(s) of non-maternal zooids (Figs 48, 55, 66 and 79). It may therefore be inferred that there is a distinct pause between the development of the maternal zooid and its corresponding ovicell, caused by the discontinuous growth of the colony. Although it is perhaps more usual for an ovicell of category A to be produced just one autozooid generation after the maternal zooid, a delay greater than one autozooid generation may be inferred in some cases. For instance in Figure 79, zooid 1 is a maternal zooid which contributed to the budding of completed zooid 2, and both 1 and 2 are contributing to the budding of 3. The ovicell within which an embryo produced by zooid 1 would be brooded is not yet fully developed, being a proximal component of zooid 3, two autozooid generations later than 1. It is apparent that the U-shaped distal pore (? pore chamber window) of the maternal zooid is responsible for the production of an ovicell during the budding of a later zooid, so that the ovicell always lies immediately distal to the orifice of the maternal zooid. If the maternal zooid is involved in the budding of more than one subsequent zooid, it is the daughter zooid to which the U-shaped distal pore contributes that bears the ovicell. Thus in Figure 79 maternal zooid 1 has contributed to the budding of zooid 2 through one or more distolateral pore chambers and to the budding of zooid 3 through the U-shaped distal pore; accordingly, the ovicell is part of zooid 3. Although the ovicell usually lies at the proximal end of the distal zooid in a more or less median position, it may be displaced some distance from the proximal end and lie to one side or other of the frontal shield if the spatial packing of the zooids dictates this (compare the two ovicells in Figure 43).

In species with ovicells of category C, ontogenetically complete maternal autozooids are rarely if ever seen on the edge of the colony without a developing or complete ovicell. Thus any pause between the development of the maternal autozooid and the ovicell must be very short, and the process of budding of the autozooid and ovicell is more or less integrated. In this way ovicells of category C are produced earlier, in terms of autozooid generations, than those of category A, and brooding may presumably commence correspondingly sooner.

### Acknowledgements

We thank P. D. Taylor, P. J. Chimonides, P. L. Cook and S. Lidgard for their comments on the manuscript. E. Buge, J. L. d'Hondt, M. V. Hounsome, W. Schedl and N. Vávra kindly arranged loans of specimens. J. G. Harmelin and J. Aristegui provided encouragement and advice, and JGH lent material from his own collections. The International Commission on Zoological Nomenclature were consulted on the date of establishment of *Cribrilaria*. We are grateful to the staff of the Electron Microscopy Unit and the Photographic Unit at the BMNH for considerable help.

### References

- Aristegui, J. 1983. *Estudio Faunístico y Ecológico de los Briozoos Quilostomados (Ectoprocta, Cheilostomata) del Círculo de Tenerife*, 1-266. Memoria de Licenciatura, Facultad de Biología, Universidad de La Laguna.

- 1984. *Bryozoos Quilostomados (Ectoprocta, Cheilostomata) de Canarias: Estudio Sistemático, Faunístico y Biogeográfico*, i-iii and 1-524. Tesis Doctoral, Facultad de Biología, Universidad de La Laguna.
- Banta, W. C. & Carson, R. J. M.** 1978. Bryozoa from Costa Rica. *Pacific Science* **31**: 381-424.
- Barroso, M. J.** 1919. Notas sobre bryozoos españoles. *Boletín de la Real Sociedad Española de Historia Natural* **19**: 340-347.
- Bishop, J. D. D.** 1986. The identity of *Cribrilaria innominata* (Couch, 1844) (Bryozoa, Cheilostomata). *Bulletin of the British Museum (Natural History), Zoology Series* **50**: 93-102.
- Busk, G.** 1854. *Catalogue of Marine Polyzoa in the Collection of the British Museum. Part 2. Cheilostomata (part.)*, i-viii and 55-120. London.
- 1859. *A Monograph of the Fossil Polyzoa of the Crag*, i-xiii and 1-136. London.
- Canu, F. & Bassler, R. S.** 1925. Les bryozoaires du Maroc et de Mauritanie. 1er Mémoire. *Mémoires de la Société des Sciences Naturelles (et Physiques) du Maroc* **10**: 1-79.
- & — 1928. Les bryozoaires du Maroc et de Mauritanie. 2e Mémoire. *Mémoires de la Société des Sciences Naturelles (et Physiques) du Maroc* **18**: 1-85.
- & — 1929. Bryozoaires éocènes de la Belgique conservés au Musée Royal d'Histoire naturelle de Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique* **39**: 1-68.
- & — 1929a. Bryozoa of the Philippine region. *Bulletin of the United States National Museum* **100** (9): i-xi and 1-685.
- Couch, R. Q.** 1844. *A Cornish Fauna. Part 3. The Zoophytes and Calcareous Corallines*, i-xvii and 1-164. Truro.
- David, L. & Pouyet, S.** 1974. Révision des bryozoaires cheilostomes miocènes du Bassin de Vienne—Autriche. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon* **60**: 83-257.
- Eggleston, D.** 1969. Marine fauna of the Isle of Man: revised lists of phylum Ectoprocta (= Kamptozoa) and phylum Ectoprocta (= Bryozoa). *Report of the Marine Biological Station at Port Erin* **81**: 57-80.
- Gautier, Y. V.** 1956. Résultats scientifiques des campagnes de la *Calypso*. 2. Études sur l'îlot du Grand Congloué (Archipel de Riou, près Marseille). 5. Bryozoaires. *Annales de l'Institut Océanographique* **32**: 189-225.
- 1962. Recherches écologiques sur les bryozoaires chilostomes en Méditerranée occidentale. *Recueil des Travaux de la Station Marine d'Endoume* **38**: 1-434.
- Godwin, D. P.** 1984. The marine fauna of New Zealand: Bryozoa: Gymnolaemata from the Kermadec Ridge. *New Zealand Oceanographic Institute Memoir* **91**: 1-198.
- Grant, A. & Hayward, P. J.** 1986. Bryozoan benthic assemblages in the English Channel. Pp. 115-124 in: Nielsen, C. & Larwood, G. P. (Eds). *Bryozoa: Ordovician to Recent*. Fredensborg.
- Harmelin, J. G.** 1968. Bryozoaires récoltés au cours de la campagne du *Jean Charcot* en Méditerranée orientale (août-septembre 1967). 1. Dragages. *Bulletin du Muséum National d'Histoire Naturelle (2e Série)* **40**: 1179-1208.
- 1970. Les *Cribrilaria* (bryozoaires chilostomes) de Méditerranée; systématique et écologie. *Cahiers de Biologie Marine* **11**: 77-98.
- 1978. Sur quelques cribrimorphes (Bryozoa, Cheilostomata) de l'Atlantique oriental. *Téthys* **8**: 173-192.
- 1984. Bryozoaires des peuplements sciaphiles de Méditerranée: révision de *Cribrilaria setosa* Waters et description de deux nouvelles espèces de *Cribrilaria* (Bryozoa, Cheilostomata). *Zoologica Scripta* **13**: 81-88.
- Harmer, S. F.** 1926. The Polyzoa of the Siboga Expedition. Part 2. Cheilostomata Anasca (with additions to previous reports). *Siboga-Expeditie* **28b**: i-viii and 181-501.
- Hayward, P. J. & Cook, P. L.** 1983. The South African Museum's *Meiring Naude* Cruises. Part 13. Bryozoa 2. *Annals of the South African Museum* **91**: 1-161.
- & **Ryland, J. S.** 1978. Bryozoa from the Bay of Biscay and Western Approaches. *Journal of the Marine Biological Association of the United Kingdom* **58**: 143-159.
- & — 1979. British ascophoran bryozoans. *Synopsis of the British Fauna (New Series)* **14**: 1-312.
- Heller, C.** 1867. Die Bryozoën des adriatischen Meeres. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* **17** (Abhandlungen): 77-136.
- Hincks, T.** 1880. *A History of the British Marine Polyzoa* **1**: i-cxli and 1-601; **2**: 83 pl. London.
- 1883. Report on the Polyzoa of the Queen Charlotte Islands. *Annals and Magazine of Natural History, Series 5* **11**: 442-451.
- Holme, N. A.** 1966. The bottom fauna of the English Channel. Part 2. *Journal of the Marine Biological Association of the United Kingdom* **46**: 401-493.
- d'Hondt, J. L.** 1970. Campagne d'essais du *Jean Charcot* (3-8 décembre 1968). 5. Bryozoaires. *Bulletin du Muséum National d'Histoire Naturelle (2e Série)* **42**: 232-256.

- 1979. Bryozoen aus dem Nordatlantik und dem Englischen Kanal. 'Meteor' Forschungsergebnisse, Reihe D 28: 1–5.
- Johnston, G.** 1847. *A History of the British Zoophytes* (2nd edition) 1: i-xvi and 1–488; 2: 74 pl. London.
- Jullien, J.** 1886. Les Costulidées, nouvelle famille de bryozoaires. *Bulletin de la Société Zoologique de France* 11: 601–620.
- Kirkpatrick, R.** 1888. Polyzoa of Mauritius. *Annals and Magazine of Natural History, Series 6* 1: 72–85.
- Landsborough, D.** 1852. *A Popular History of British Zoophytes, or Corallines*, i-xii and 1–404. London.
- Levensen, G. M. R.** 1909. *Morphological and Systematic Studies on the Cheilostomatous Bryozoa*, i-vii and 1–431. Copenhagen.
- Lidgard, S.** 1985. Zooïd and colony growth in encrusting cheilostome bryozoans. *Palaeontology* 28: 255–291.
- Manzoni, A.** 1871. Supplemento alla fauna dei bryozoi Mediterranei. 1a Contribuzione. *Sitzungsberichte der Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe. Wien. Abt. 1* 63: 73–82.
- Norman, A. M.** 1903. Notes on the natural history of East Finmark. *Annals and Magazine of Natural History, Series 7* 12: 87–128.
- Osburn, R. C.** 1950. Bryozoa of the Pacific coast of America. Part 1, Cheilostomata-Anasca. *Allan Hancock Pacific Expeditions* 14: 1–269.
- Prenant, M. & Bobin, G.** 1966. Bryozoaires. 2. Chilostomes Anasca. *Faune de France* 68: 1–647.
- Reuss, A. E.** 1848. Die fossilen Polyparien des Wiener Tertiärbeckens. *Naturwissenschaftliche Abhandlungen. Wien* 2: 1–109.
- Simpson, G. G., Roe, A. & Lewontin, R. C.** 1960. *Quantitative Zoology*, i-vii and 1–440. New York.
- Soule, J. D.** 1959. Results of the Puritan-American Museum of Natural History expedition to western Mexico. 6. Anascan Cheilostomata (Bryozoa) of the Gulf of California. *American Museum Novitates* 1969: 1–54.
- Thornely, L. R.** 1912. The marine Polyzoa of the Indian Ocean, from H.M.S. *Sealark*. *Transactions of the Linnean Society of London, 2nd Series, Zoology* 15: 137–157.
- Waters, A. W.** 1879. On the Bryozoa (Polyzoa) of the Bay of Naples. *Annals and Magazine of Natural History, Series 5* 3: 28–43.
- 1899. Bryozoa from Madeira. *Journal of the Royal Microscopical Society* 1899: 6–16.
- Winson, J. E.** 1984. Shallow-water bryozoans of Carrie Bow Cay, Belize. *American Museum Novitates* 2799: 1–38.
- 1986. Bryozoans from Bali, Lombok and Komodo. *American Museum Novitates* 2847: 1–49.